

Covariance functions, genetic parameters and breeding values for longitudinal ultrasound measures of rib eye area in a Colombian *Bos indicus*-*Bos taurus* multibreed cattle population using random regression models

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ABSTRACT

The objective of this research was to obtain restricted maximum likelihood estimates of covariance functions and predictions of breeding values for longitudinal records of rib eye area measured by ultrasound (REA) in a Colombian multibreed cattle population. The dataset contained 708 records from 340 calves progeny of 37 sires from nine breeds (Gray Brahman, Red Brahman, Guzerat, Blanco Orejinegro, Romosinuano, Braunvieh, Normand, Limousine and Simmental) mated to Gray Brahman Cows. The mixed model was a random regression model that used Legendre polynomials (LP) of order 1 to 3. Fixed effects were age of animal, dam parity, contemporary group (herd*year*season*sex), breed additive genetic and heterosis, while direct and maternal additive genetic and maternal permanent environment were random effects. Residual variances were modeled either as constant or changing across the growth trajectory. Models were compared with the corrected Akaike’s Information criteria and the Schwartz’s Bayesian information criteria. According to these criteria the best model was the one with first order LP and constant residual variance. Thus, this model was used to obtain genetic parameters and breeding values. Direct additive genetic variance decreased until 156 d and then increased. Maternal additive genetic and maternal permanent environment variances increased with age. Direct heritability estimates for REA at 4 mo, weaning, 12 and 15 mo (considered as target ages) were 0.004, 0.01, 0.03 and 0.06, respectively. Maternal heritabilities for the same ages were 0.32, 0.35, 0.37 and 0.38. Direct additive correlations ranged from -0.7 to 1. Maternal additive genetic and permanent environmental correlations were close to unity across the entire range of ages. Results suggested that selection for maternal ability in this multibreed population was feasible and that maternal effects (genetic and environmental) had an important influence on REA in pre and postweaning stages. Validation of these results with larger multigenerational multibreed populations is needed.

Key words: carcass composition, covariance functions, crossbred cattle, ultrasound

INTRODUCTION

Kirkpatrick et al. (1990) proposed modeling longitudinal records with Legendre polynomials (LP) to describe direct additive genetic covariances among records at any pair of ages in a continuous form. The LP are solutions to the Legendre’s differential equation and they are orthogonal. This property allows describing patterns of genetic variation trough a growth trajectory. Continuous functions representing covariances among records are known as covariance functions (Kirkpatrick et al., 1990). Meyer (1998) suggested that coefficients of covariance functions could be estimated as covariances among random regression coefficients by fitting linear mixed models. Advantages of random regression over multiple trait models involve the inclusion of all available data without pre-adjustment to particular ages, no lose of records taken outside certain age ranges, and reduction in the number of parameters to be estimated by fitting parsimonious models (Kirkpatrick et al., 1990; Meyer and Hill, 1997).

Because carcass quality is very important in the current beef market, there exists great interest in carcass traits measured by ultrasound like the rib eye area (REA), because they are closely related to the actual carcass values and meat yields. Genetic evaluation of carcass traits has been implemented in animal breeding programs in different countries and species (Fischer et al., 2006; Choy et al., 2008). However, few genetic studies have considered ultrasound carcass traits in a longitudinal manner either in purebred or crossbred cattle (Fischer et al., 2006; Mercadante et al., 2010). Jimenez et al. (2010) conducted the only study in Colombia on ultrasound carcass traits in cattle under pasture conditions using purebred Brahman. In low tropical areas of Colombia crossbreeding between native or European (*Bos taurus*) with Zebu (*Bos indicus*) breeds is frequently used as a strategy to increase beef production while maintaining adaptability. This mating strategy has created a need to establish genetic evaluation programs involving animals from temperate and tropically adapted breeds for carcass traits. These programs have to take into account that 72% of the Colombia’s cattle population is Zebu (mainly Brahman. Thus, the objective of this research was to obtain restricted maximum likelihood estimates of covariance functions and genetic parameters, and best linear unbiased predictions of breeding values for longitudinal REA records in a multibreed cattle population in a low tropical area of Colombia.

MATERIALS AND METHODS

All of the practices involving manipulation of animals that were performed to obtain records in this research were approved by the Animal Bioethics Committee of the National University of Colombia (Approval letter number: CBE-FMVZ-012, July of 2010).

Breeds, matings and animal’s management. To construct the multibreed population, 37 bulls from 9 breeds were sired to first-parity Gray Brahman cows and heifers. Sire breeds were Gray Brahman (GB), Red Brahman (RB), Guzerat (GUZ), Romosinuano (ROM), Blanco Orejinegro (BON), Simmental (SIM), Braunvieh (BVH), Normand (NOR) and Limousin (LIM). These *Bos taurus* breeds (native and temperate) were chosen because they are frequently used for crossbreeding programs with zebu cattle in Colombia’s low tropical beef production systems. Brahman was included because it has the largest cattle population in the country (Jiménez et al., 2010), and GUZ is a *Bos indicus* breed with increasingly higher representation in Colombia that has not been studied as a single breed or in crosses with Brahman. Females were chosen on the basis of a normal reproductive cycle and a healthy reproductive system. Once selected, females were randomly allocated to males, and artificially inseminated using a fixed-time protocol. Calves were born in 2009 and 2010. Table 1 shows the number of sires per breed and the number of calves per breed group by year and total. Animals were kept in two herds located in Southern Cesar, in the municipality of Aguachica, Colombia. The ecosystem in this micro region is a very dry tropical forest. This region has a mean annual temperature of 28 °C, a height above sea level of 50 m, a relative humidity of 80% and sandy-loam soils. Because of its environmental conditions, Southern Cesar is considered to be better suited for beef cattle production than other areas in Colombia.

Table 1. Number of sires per breed and number of calves per breed group and birth year

| ¹Sire Breed | Number of sires | Breed group of calf | Number of calves | | |
|-------------|-----------------|---------------------|------------------|------|-------|
| | | | 2008 | 2009 | TOTAL |
| BON | 3 | BON × GB | 21 | 12 | 33 |
| BVH | 3 | BV × GB | 13 | 8 | 21 |
| GB | 12 | GB × GB | 63 | 34 | 97 |
| GUZ | 3 | GUZ × GB | 18 | 9 | 27 |
| LIM | 3 | LIM × GB | 20 | 13 | 33 |
| NOR | 3 | NOR × GB | 22 | 14 | 36 |
| RB | 4 | RB × GB | 26 | 8 | 34 |
| ROM | 3 | ROM × GB | 18 | 10 | 28 |
| SIM | 3 | SIM × GB | 21 | 10 | 31 |
| TOTAL | 37 | | 222 | 118 | 340 |

¹BON = Blanco Orejinegro; BVH = Braunvieh; GB = Gray Brahman; GUZ = Guzerat; LIM = Limousin; NOR = Normand; RB = Red Brahman; ROM = Romosinuano; SIM = Simmental

feeding was based on pastures. Grass species were Brachipará (*Brachiaria plantaginea*), Guinea (*Panicum máximum*) and Angleton (*Dichanthium aristatum*). Pastures were not fertilized. Animals were provided with an 8% phosphorus mineral supplement (GANASAL®, Colombia). Mineral supplement consumption was *ad libitum*. The grazing system was rotational with a rotation period of 60 d. All calves were weaned between 7 and 8 mo of age and males were castrated at 12 mo of age.

Records. Rib eye area records were taken by a certified technician of the Colombian Zebu Cattle Breeders Association ASOCEBU, (ASOCEBU, Bogotá D.C., Colombia) using an Aquila Esaote model device (Pie Medical Equipment B.V., Maastricht, Limburg, The Netherlands). Once ultrasound images were collected, they were analyzed to check quality and to obtain the REA values (cm²) using the Echo Image Viewer software of Pie Medical (Pie Medical Equipment B.V., Maastricht, Limburg, The Netherlands). The total number of REA records was 708. Age of animals ranged from 70 to 492 d and all animals had records at several ages. Records were intended to be taken approximately at four, eight (weaning), twelve and fifteen mo. Mean ages at each of these data collection points were: 120, 233, 332 and 445 d.

Genetic-Statistical Analyses. Mixed models procedures were carried out to obtain restricted maximum likelihood (REML) estimates of covariance components and best linear unbiased predictors (BLUP) of animal breeding values (BV). Normalized (with norm 1) LP evaluated at age of animal when data were collected were used as regression variables to estimate covariance functions (CF) for direct additive genetic (DAGCF), maternal additive genetic (MAGCF) and maternal permanent environment (MPECF) and to compute BV. Orders of polynomials ranged from 1 to 3. The following combinations of LP to describe direct additive, maternal additive and maternal permanent environment CF were used: one (LP1), 2 (LP2) and 3 (LP3) for the 3 covariance components, 3 for direct additive genetic covariances and 2 for maternal additive genetic and permanent environment covariances (LP32). The residual variance was modeled in two ways. The first one assumed that the residual variance was the same along the entire growth trajectory (LP1HOM, LP2HOM, LP3HOM, LP32HOM), and the second one assumed a step function (LP1HET, LP2HET, LP3HET, LP32HET) across 3 age intervals: 70 ≤ age ≤ 230 d, 230 < age ≤ 365 d and 365 < age ≤ 492 d. Residuals were assumed to be independent and normally distributed. Thus, there were a total of 8 random regression models (RRM) to compare: LP1HET, LP2HET, LP3HET, LP32HET, LP1HOM, LP2HOM, LP3HOM, and LP32HOM. In matrix notation the general model was as follows: $y = X\beta + Q_{ga}g_{at} + Q_nh + \Phi_a a + \Phi_m m + \Phi_p p + e$ with moments: $E[y] = X\beta + Q_{ga}g_{at} + Q_nh$ and $Var[y] = \Phi_a A \otimes K_a \Phi'_a + \Phi_m A \otimes K_m \Phi'_m + \Phi_p I \otimes K_p \Phi_p$

Where y = vector containing the REA records, β = vector of unknown fixed effects of contemporary group, dam parity and age of animal, g_{at} = vector of fixed additive genetic group effects (modeled as a continuous function of the time), h = vector of fixed non additive genetic effects (individual heterosis), a = vector of random regression coefficients for direct additive genetic effects, m = vector with random regression coefficients for maternal additive genetic effects, p = vector containing random regression coefficients for maternal permanent environmental effects, and e = random vector of residuals, X, Q_{ga}, Q_n, Φ_a, Φ_m, and Φ_p were known incidence matrices respectively relating vectors β, g_{at}, h, a, m, and p to REA records. Columns in matrix X relating records to fixed effects of age contained second order LP evaluated at each age; columns for the other fixed effects contained zeroes and ones. Matrix Q_{ga} contained linear LP evaluated at the expected fraction of each breed in an animal times the age of the animal, matrix Q_n contained probabilities of alleles of different breeds occurring at one locus in the animal and the matrices Φ_a, Φ_m, and Φ_p contained LP evaluated at the ages of the animals when records were taken. Matrices K_a, K_m and K_p contained the coefficients for additive genetic, maternal additive genetic and maternal permanent environmental covariance functions, the matrix A was the additive relationship matrix, symbol⊗ represented the Kronecker product and R the residual covariance matrix which had the form $R = I\sigma_e^2$ for models LP1HOM, LP2HOM, LPHOM and LP32HOM and $R = diag(\sigma_{e_l}^2), l = 1, 2, 3$ for the models LP1HET, LP2HET, LP3HET, and LP32HET, with sub index l denoting the lth age interval.

Analyses were performed with software WOMBAT (Meyer, 2007) using an average information (AI) algorithm. Convergence was declared when change of value of the natural logarithm of the restricted likelihood function in two consecutive iterations was lower than 5*10⁻⁴. Models were compared through the Schwartz’s Bayesian Information Criterion (BIC) and the Corrected Akaike’s Information Criterion (AICC). Once best RRM was selected, matrices of covariance components for additive direct genetic effects, additive maternal genetic effects, and maternal permanent environmental effects as well as BV for REA at 4 target ages were obtained using the REML estimates of covariance matrices among random regression coefficients obtained at convergence which are equal to the coefficient matrices of corresponding CF (Meyer, 1998). Target ages were 120, 230, 365 and 450 d, and the corresponding REA values were denoted as REA4, REAW, REAY and REAF. The additive BV for each animal were computed by adding two terms. The first one was a weighted sum of probabilities of alleles of each breed in the animal and the second was the BLUP of the random solution for each individual which was computed as the internal (or dot) product between a vector containing LP evaluated at each age and a vector whose entries were the BLUP for random regression coefficients of the animal.

RESULTS AND DISCUSSION

Model LP1HOM was the selected one as it had the lowest AICC and BIC values (Table 2). Selection of the most parsimonious model implies that the larger log likelihood values obtained with other models was insufficient to counterbalance BIC and AICC penalties due to the higher number of parameters. Thus the BIC and AICC values of those other models were larger than the values for model LP1HOM. Direct additive genetic covariance function had a saddle point located at 156 days. Thus, covariances before 156 days tended to decrease with age. After 156 d, the pattern was more complex. Covariances among ages lower than 156 d and ages greater than 156 d tended to decrease when distance among them increased. Covariances among ages greater than 156 d tended to increase as the animals grew older. Maternal additive genetic covariance function increased as the distance among age points increased, except towards the end of the growth trajectory where it decreased quickly. The MAGCF and MPECF were positive throughout the entire domain. The behavior of MPECF function tended to be opposite to MAGCF. When MAGCF had high values, MPECF values were low (Figures), and at high age values MAGCF decreased quickly whereas MPECF increased quickly. Restricted maximum likelihood estimate of residual variance was 25.57 cm⁴. Phenotypic covariance also increased as animals grew older. Its minimum value was 45.5 cm⁴ at 70 d and its maximum was 65.43 cm⁴ at 492 d. Direct additive genetic variance (DAGV) had a global minimum located at 156 days (0.15 cm⁴). The largest value of DAGV was 4.63 cm⁴ at 492 d. Maternal additive genetic variance increased with age. Its minimum value was 13.87 cm⁴ at 70 d and its maximum value was 24.89 cm⁴ at 492 d. Maternal permanent environmental variance had its maximum value at 492 d (10.33 cm⁴) and the minimum (5.64 cm⁴) at 70 d. Direct heritability (Dh) estimates were low at the entire trajectory. The Dh reached a global minimum at 156 d (0.003) and its maximum at 492 d (0.071). Maternal heritabilities were considerably higher than Dh through the entire growth trajectory. They were moderate and increased with age of animal. The ratio of MPEV to phenotypic variance ranged from 0.12 at 70 d to 0.16 at 492 d. Covariances and genetic parameters for the five target ages are presented in (Table 3).

Direct additive genetic correlations estimates (DAGR) formed a plateau close to unity approximately after 211 days among. On the other hand, DAGR among REA at 70 days and REA at other ages were negative after 200 days and had its lowest value at 492 days (-0.7). The maternal additive and maternal permanent environmental correlations were close to unity throughout the entire range of ages considered. The Phenotypic correlation estimates were always positive and ranged from moderate to high. Overall mean BV were 0.41 cm² for REA4, 0.72 cm² for REAW, 1.26 cm² for REAY and 1.55 cm² for REAF. Results suggested that on average LIM bulls had the highest BV for REA. Sires of BVH and NOR breeds had the smallest BV at the 4 target age points. In the Criollo cattle group, ROM sires had greater mean BV than BON sires. Finally, for the Bos indicus breeds, GUZ bulls had the greatest mean BV.

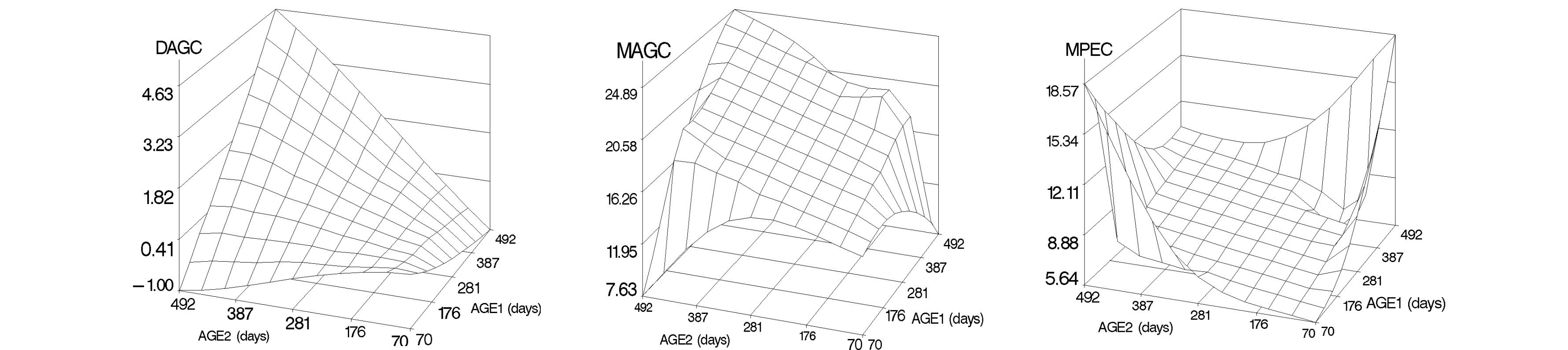
Table 2. Akaike’s corrected information criterion (AICC), Schwartz’s Bayesian information criterion (BIC), residual analysis and number of parameters for each model.

| Model | AICC | BIC | Number of parameters | Log L ¹ |
|---------|---------|---------|----------------------|--------------------|
| LP1HET | 3394.74 | 3448.66 | 12 | -1685.15 |
| LP2HET | 3412.64 | 3506.42 | 21 | -1684.65 |
| LP3HET | 3435.54 | 3581.68 | 33 | -1683.10 |
| LP32HET | 3426.62 | 3555.42 | 29 | -1683.03 |
| LP1HOM | 3392.82 | 3437.8 | 10 | -1686.25 |
| LP2HOM | 3410.66 | 3495.62 | 19 | -1685.78 |
| LP3HOM | 3508.34 | 3645.82 | 31 | -1721.70 |
| LP32HOM | 3426.66 | 3546.72 | 27 | -1685.22 |

| | REA4 | REAW | REAY | REAF |
|------|-------|-------|-------|-------|
| REA4 | 0.004 | 0.16 | -0.24 | -0.32 |
| | 0.32 | 0.99 | 0.99 | 0.99 |
| REAW | 0.04 | 0.01 | 0.92 | 0.88 |
| | 16.28 | 0.35 | 0.99 | 0.99 |
| REAY | -0.15 | 0.76 | 0.03 | 1 |
| | 17.85 | 19.37 | 0.37 | 0.99 |
| REAF | -0.27 | 1.01 | 2.59 | 0.06 |
| | 18.84 | 20.44 | 22.41 | 0.38 |

¹On Diagonals: Top direct heritabilities, bottom maternal heritabilities, over diagonal: top: direct additive genetic correlations, bottom maternal additive genetic correlations, below diagonal: top: direct additive genetic covariances, bottom: maternal additive genetic covariances

¹Natural logarithm of the restricted likelihood function



FINAL REMARKS

It should be considered that genetic parameters and breeding values were estimated with limited accuracy because of the structure and small size of the multibreed population. Results suggested that maternal effects were important both at pre-weaning and post-weaning growth stages. Thus, maternal effects appeared to be relevant effects to be included in models for genetic evaluation of REA pre and post-weaning under Colombian low tropical pasture conditions. The BLUP of BV suggested that LIM bulls had the greatest mean genetic merit for REA at all target ages. When all of the sires were ranked according to individual BV, LIM sires were always those with the greatest values. Consequently, the LIM breed would have to be considered for crossbreeding programs with Brahman cows under pasture conditions in the Southern Cesar region of Colombia. It is necessary to validate the results of this research with substantially larger multigenerational populations. Thus, there is a need to continue obtaining longitudinal ultrasound information in the country.

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