



Genetic evaluation of partial growth trajectory of Santa Inês breed using random regression models

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ABSTRACT - It was evaluated data set of 19,303 weight records of Santa Inês sheep in order to evaluate distinct polynomial functions with different order for better adjustments of fixed and random regressions of growth trajectory and to estimate (co)variances components and genetic parameters of this trajectory. Fixed effects used in analysis were contemporary group, sex and birth type. Ordinary and Legendre polynomials, ranging from two to four orders, were evaluated for fixed regression of average growth trajectory. Legendre and quadratic b-spline functions, ranging from three to four orders, were evaluated for random regressions. Legendre polynomials of order fourth were suitable to fit random regression, while ordinary polynomials of third order were the best for fixed trajectory. Direct heritabilities on days 1, 50, 150, 250 and 411 were 0.24, 0.12, 0.44, 0.84, and 0.96, respectively, while maternal heritabilities for the same ages were 0.24, 0.19, 0.09, 0.02, and 0.01, respectively. Genetic correlations among weights in subsequent ages were high, tending to unity, and there were negative correlations between weights at early ages and weights at late ages. It is possible to modify the growth trajectory by selection with the observed genetic variability. Genetic control of weights at initial ages is not the same in late ages. So, selection of animals for slaughter in early age must be different from that of replacement animals.

Key Words: β -spline functions, genetic correlation, heritability, Legendre polynomials, ordinary polynomials

Avaliação genética de parte da trajetória de crescimento em ovinos da raça Santa Inês utilizando modelos de regressão aleatória

RESUMO - Foram utilizados 19.303 registros de peso de ovinos da raça Santa Inês com os objetivos de avaliar funções polinomiais com diferentes ordens para melhor ajuste das regressões fixas e aleatórias da trajetória de crescimento e estimar os componentes de covariância e os parâmetros genéticos desta trajetória. Os efeitos fixos utilizados nas análises foram grupo de contemporâneos, sexo e tipo de nascimento. Para ajuste da regressão fixa da trajetória média de crescimento, foram avaliados polinômios ordinários e de Legendre com ordens variando de 2 a 4. Para as regressões aleatórias, foram avaliadas as funções de Legendre e β -spline quadrática, com ordens variando de 3 a 4. As funções com polinômios de Legendre de quarta ordem foram adequadas para ajustar a parte aleatória, enquanto os polinômios ordinários de terceira ordem foram melhores para ajustar a parte fixa. As herdabilidades diretas nos dias 1, 50, 150, 250 e 411 foram de 0,24; 0,12; 0,44; 0,84; e 0,96, respectivamente, enquanto as herdabilidades maternas nessas idades foram de 0,24; 0,19; 0,09; 0,02 e 0,01. As correlações genéticas entre pesos em idades subsequentes foram elevadas, tendendo à unidade, e houve correlações negativas entre pesos tomados em idades mais jovens e aqueles tomados em idades mais avançadas. A variabilidade genética observada permite alterar a trajetória de crescimento por meio de seleção. O controle genético dos pesos nas fases iniciais do crescimento não é o mesmo que atua em idades mais tardias. Assim, a seleção de animais para abate em idade jovem deve ser diferente daquela para animais de reposição no rebanho.

Palavras-chave: correlação genética, funções β -spline, herdabilidade, polinômios de Legendre, polinômios ordinários

Introduction

Estimates of genetic parameters are of paramount importance to design effective strategies for animal selection. Concerned to meat sheep, body weight is the main trait evaluated for selection. Weights are taken at different ages and they are usually evaluated as distinct traits, such as

repeated measures or longitudinal data characterized by clusters of observations from several measurements taken in the same individual over time. Currently, these traits are being evaluated as infinite-dimensional characters, in which the phenotype of an animal is described as a function, much more than a finite number of measurements (Kirkpatrick & Heckman, 1989). According to these authors, these models

are more advantageous for covering the entire range of continuous taken measures, allowing to predict the breeding value of animals anywhere in that range.

The use of random regression models has the advantages of improving use and adjustment of data because all the measures of the animal and its relatives are used for evaluation and enhance the accuracy of selection. According to Meyer (2000), these models accommodate repeated records for traits that gradually change over time and require no assumptions about the constancy of variances and correlations; they are special cases of covariance functions that allow a direct estimate of the coefficients of covariance functions by the method of restricted maximum likelihood (Meyer & Hill, 1997; Meyer, 1998), i.e., they evaluate genetic gains and propose different objectives and selection criteria.

In Brazil, concerned to sheep, it is still demanding the use of these models, which emphasizes the need for further studies of its use. So, this study aimed to accomplish a genetic-quantitative evaluation of part of the growth curve of Santa Inês by evaluating different functions with different polynomial orders for the best fit of the fixed portion of this growth and better modeling the random portion of this trajectory and estimate its (co) variance and genetic parameters.

Material and Methods

Data were obtained from Gaasa Agropecuária Ltda, supported by Programa de Melhoramento Genético de Caprinos e Ovinos de Corte (GENECOC - Breeding Program for Meat Goats and Sheep) of Embrapa Caprinos e Ovinos (Goats and Sheep National Research Center). This flock is located in Inhumas, GO, Brazil (Altitude - 770 m, Latitude - 16° 21' 28" S and Longitude - 49° 29' 45" W; climate - Hot Tropical Semi-Wet).

It was evaluated 19,303 records of weights from birth to 411 days of age of 2,002 Santa Inês lambs born between 1996 and 2008 (Table 1). Pedigree consisted of 2,563 animals with 33 rams. Only animals with at least four weights (maximum of 70 days between measurements) were considered.

Previous analyses defined the set of fixed effects for data adjustment using the MIXED procedure of SAS software (SAS Institute Inc., 1996). The fixed effects used in the analyses were contemporary group (animals born in the same year and season), sex and birth type (single, twin, triplet).

It was evaluated 24 models with different orders to verify simultaneously the best fit for the fixed mean growth

trajectory and for the random regression of the additive direct and maternal genetic effects and the permanent environmental effects of the animal. To adjust the fixed mean growth trajectory, ordinary and Legendre polynomials, with orders ranging from two (linear) to four (cubic), were evaluated. For the random regressions, Legendre polynomial and b-spline quadratic functions, with orders ranging from three (square) to four (cubic), were evaluated.

Therefore, the general model can be represented by:

$$y_{ij} = F_{ij} + \sum_{m=0}^{k_{\beta}-1} \beta_m \phi_m + \sum_{m=0}^{k_{\alpha}-1} \alpha_{im} \phi_m + \sum_{m=0}^{k_{\gamma}-1} \gamma_{im} \phi_m + \sum_{m=0}^{k_c-1} p_{im} \phi_m + \varepsilon_{ij}$$

where:

Y_{ij} = weight j of animal i ; F_{ij} = the set of fixed effects included in the model (contemporary groups, constituted by year and season of birth, birth type and sex of lamb); ϕ_m = ordinary or Legendre polynomial, or β -spline quadratic function m of standardized age (-1 up to +1), according to evaluated model; β_m = fixed regression coefficients to fit the fixed mean growth trajectory of population; α_{im} , γ_{im} and p_{im} = the random regression coefficients to the additive direct and maternal genetic effects, and permanent environmental effects of animal, respectively, specifically for each lamb; k_{β} , k_{α} , k_{γ} and k_c = the orders of fitting for the corresponding polynomials ($2 \leq k_{\beta} \leq 4$, $3 \leq k_{\alpha}$, k_{γ} , $k_c \leq 4$); ε_{ij} = the random residual effect.

In matrix, the analysis model can be described as the following:

$$y = X \beta + Z_1 \alpha + Z_2 \gamma + Z_3 p + \varepsilon$$

where:

y = the vector with N records of ND animals; β = the vector of fixed effects, including the fixed regression coefficients; α = the vector $k_{\alpha} \times N_d$ of random regression coefficients for the additive direct genetic effects, where $N_d > ND$ denotes the total number of animals in the analysis, including ram without records; γ = the vector $k_{\gamma} \times ND$ of random regression coefficients for the additive maternal genetic effects; p = the vector $k_c \times ND$ of random regression coefficients for the permanent environmental effects of animal; ε = the vector

Table 1 - Structure of the analyzed databank

	Number	(%)
Total of records	19,303	-
Total of animals	2,563	100
Animals with records	2,002	78.1
Animals with 4 records	168	8.4
Animals with 5 records	201	10.0
Animals with 6 records	148	7.4
From 7 up to 10 records	750	37.5
From 11 up to 20 records	691	34.5
Animals without progeny	2,002	78.1

of random errors; X, Z_1, Z_2 and Z_3 = incidence matrices for fixed regression coefficients, random regression coefficients for direct, maternal and permanent environmental effects, respectively.

$$\text{Var} \begin{pmatrix} \alpha \\ \gamma \\ \rho \\ \varepsilon \end{pmatrix} = \begin{pmatrix} k_\alpha \otimes A & 0 & 0 & 0 \\ 0 & k_m \otimes A & 0 & 0 \\ 0 & 0 & k_c \otimes I & 0 \\ 0 & 0 & 0 & R \end{pmatrix}$$

The assumptions made in relation to the vectors α, γ, ρ and ε are that they have normal distribution, with $E(\alpha) = E(\gamma) = E(\rho) = E(\varepsilon) = 0$ and $\text{Var}(\alpha) = K_\alpha \otimes A, \text{Var}(\gamma) = K_m \otimes A, \text{Var}(\rho) = K_c \otimes I$ and $\text{Var}(\varepsilon) = R = I\sigma_e^2$, with zero covariance between the vector ρ and the vectors α and γ, K_α, K_m and K_c = the matrices of variance and covariance between random regression coefficients for additive genetic and maternal effects and permanent environmental effects of animal, respectively; I = an identity matrix; σ_e^2 = the residual variance; A = the matrix of numerators of the Wright's coefficients of relationship.

The residual variance was considered heterogeneous, and five classes were used: 1) for birth weight, 2) from 2 to 60 days of age, 3) from 61 to 120 days of age, 4) 121 to 230 days of age, and 5) 231 to 411 days of age.

The analyses were performed by the method of average information restricted maximum likelihood (AIREML) using the statistical package WOMBAT 1.0 (LINUX Version), described by Meyer (2007). WOMBAT calculates many criteria (change in $\log L < 5 \times 10^{-4}$; change in parameters $< 10^{-8}$; norm of gradient vector $< 10^{-3}$) for determining when an analysis reached convergence.

The models with different orders of settings for different polynomials were compared by log-likelihood function ($\log_e L$), Akaike's Information criterion (AIC) and Schwarz's bayesian information criterion (BIC). The latter two allow the comparison among non-nested models and penalizes the most parameterized, and the BIC is more rigorous, i.e., favors parsimonious models more (Wolfinger, 1993, Nunez-Anton & Zimmerman, 2000).

The criteria and information were given by:

$$\text{AIC} = 2\log L + 2p$$

$$\text{BIC} = 2\log L + p\log(N-r)$$

Where p = the number of parameters in the model, N = the total of records and r = the rank of matrix (incidence matrix for fixed effects). The smaller values of AIC and BIC is the best fit of the model.

We also assessed whether the models presented compatible curves to the biological growth of animals.

Results and Discussion

The model that showed the highest value of log L was the model 22, with Legendre polynomials of fourth order (cubic) to adjust the fixed trajectory, and a fourth order to adjust the random trajectory (Table 2). However, this model overestimated the predicted values for body weight, for example, 12 kg for birth weight, and negative values for the final part of the curve (-59.71 kg at 411 days old). Model 6 was only model that properly set the trend of growth, with ordinary polynomials of third order (quadratic) in the fixed part and Legendre polynomials of fourth order (cubic) in the random. All other models promoted over-estimates of weights at the beginning and / or negative values at the end of the trajectory.

Weights of animals ranged from 2.91 kg at birth to 47.31 kilograms at 411 days of age (Figure 1). By assessing the observed midpoints, it can be seen that the quadratic curve fit well the data, mainly up to 150 days of age, although there are some midpoints much lower than the expected.

The behavior of the estimates was very similar between the direct and phenotypic variances and among maternal and permanent environmental variances (Figure 2). Anyway, all of them present a great increase after 250 days of age. Almost all phenotypic variances were due to additive direct effects.

The values of direct and maternal heritabilities (Figure 3) were very similar until about 35 days, then taking on antagonistic behavior. From this day until day 78, maternal heritabilities exceeded direct heritabilities. However, after 78 days, the maternal heritabilities decreased while the direct heritabilities surged. From the day 250, the maternal heritabilities were practically equal to zero.

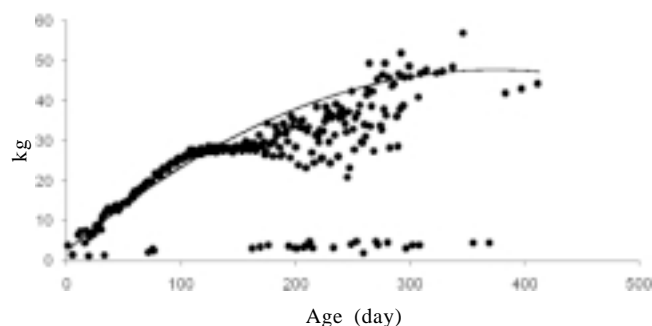


Figure 1 - Average growth trajectory estimated by random regression model with ordinary polynomials of third order (quadratic) in the fixed part and Legendre polynomials of fourth order (cubic) in the random part (model 6) and observed values (points) for the Santa Inês breed, with weights taken from birth to 411 days of age.

Table 2 - Model number, number of parameters, fixed and random functions, with their respective orders and criteria used in the choice of the best fit for the partial growth trajectory of Santa Inês breed sheep

Model	Number of parameters	Fixed part			Random part			Criteria			Observation
		Function	Order	Function	Order	Log L	1/2 AIC	1/2 BIC			
1	23	Ordinary polynomials	2	Legendre	3	-19,308.996	-19,331.461	-19,422.461	Overestimated weights		
2	35	Ordinary polynomials	2	Legendre	4	-18,057.497	-18,092.497	-18,230.162	Overestimated weights		
3	23	Ordinary polynomials	2	b-spline	3	-19,313.517	-19,336.517	-19,426.983	Overestimated weights		
4	35	Ordinary polynomials	2	b-spline	4	-19,131.644	-19,166.644	-19,304.309	Overestimated weights		
5	23	Ordinary polynomials	3	Legendre	3	-19,316.311	-19,339.311	-19,429.776	Overestimated weights		
6	35	Ordinary polynomials	3	Legendre	4	-18,043.817	-18,078.817	-18,216.481	Best fit		
7	23	Ordinary polynomials	3	b-spline	3	-19,316.300	-19,339.300	-19,429.765	Overestimated weights		
8	35	Ordinary polynomials	3	b-spline	4	-19,133.003	-19,168.003	-19,305.677	Overestimated weights		
9	23	Ordinary polynomials	4	Legendre	3	-19,316.483	-19,339.483	-19,429.947	Overestimated weights		
10	35	Ordinary polynomials	4	Legendre	4	-18,047.278	-18,082.278	-18,219.941	Negatives weights		
11	23	Ordinary polynomials	4	b-spline	3	-19,316.577	-19,339.577	-19,430.042	Overestimated weights		
12	35	Ordinary polynomials	2	b-spline	4	-19,126.453	-19,161.453	-19,299.116	Overestimated weights		
13	23	Legendre	2	Legendre	3	-19,303.873	-19,326.873	-19,417.338	Negatives weights		
14	35	Legendre	2	Legendre	4	-18,052.411	-18,087.411	-18,225.076	Negatives weights		
15	23	Legendre	2	b-spline	3	-19,308.395	-19,331.395	-19,421.860	Negatives weights		
16	35	Legendre	2	b-spline	4	-19,125.479	-19,160.479	-19,298.144	Negatives weights		
17	23	Legendre	3	Legendre	3	-19,301.408	-19,324.408	-19,414.873	Negatives weights		
18	35	Legendre	3	Legendre	4	-18,028.914	-18,063.914	-18,201.578	Negatives weights		
19	23	Legendre	3	b-spline	3	-19,306.480	-19,329.480	-19,419.945	Negatives weights		
20	35	Legendre	3	b-spline	4	-19,119.181	-19,154.181	-19,291.844	Negatives weights		
21	23	Legendre	4	Legendre	3	-19,287.154	-19,310.154	-19,400.618	Negatives weights		
22	35	Legendre	4	Legendre	4	-18,017.963	-18,052.963	-18,190.626	Overestimated weights		
23	23	Legendre	4	b-spline	3	-19,292.400	-19,315.400	-19,405.864	Negatives weights		
24	35	Legendre	4	b-spline	4	-19,097.114	-19,132.114	-19,269.777	Negatives weights		

Direct heritabilities on days 1; 50; 150; 250; and 411 were equal to 0.24; 0.12; 0.44; 0.84; and 0.96, respectively, while the maternal heritabilities at the same ages were 0.24; 0.19; 0.09; 0.02; and 0.01. It is noteworthy that there was a tendency of higher standard errors for the heritabilities of weights at the beginning or at the end of the trajectory.

Genetic correlations between birth weight and weights until day 16 decreased and became negative until day 63 (Figure 4), when they returned to grow and become positive until 178 days, returning to be negative by the end of the trajectory. The large oscillations seen in Figure 4 are because the weights in adjacent ages have higher direct genetic correlations, and the direct genetic control over the weights in the initial phase of growth differs from that of the final phase of the trajectory.

The associations among weights farther apart tend to be non-existent or antagonistic (Table 3).

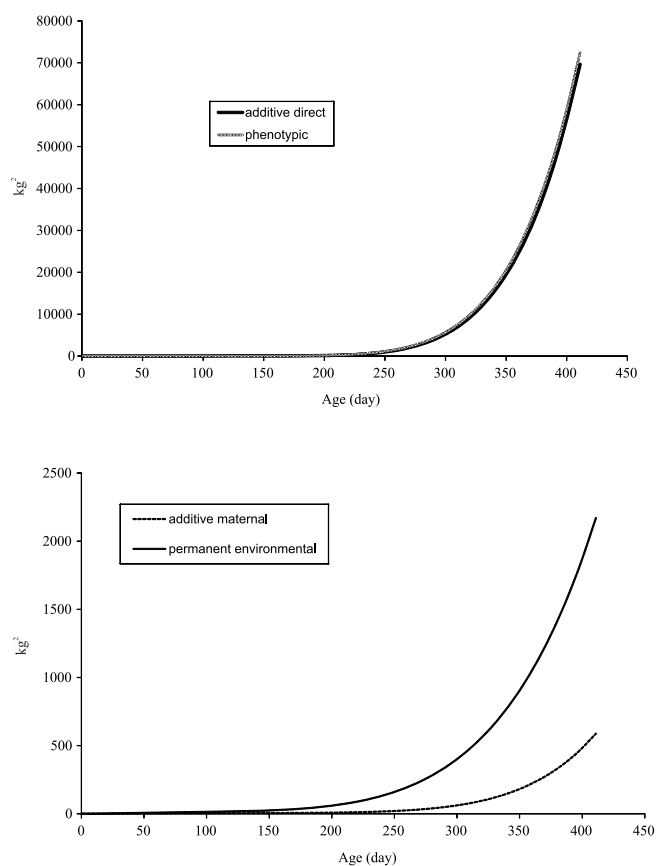


Figure 2 - Values of additive genetic direct and maternal, permanent environmental and phenotypic variances estimated by random regression model with ordinary polynomials of third order (quadratic) in the fixed part and Legendre polynomials of fourth order (cubic) in the random part (model 6), for Santa Inês breed, with weights taken from birth to 411 days of age.

The maternal correlations ranged from 0.46 (between day 1 and day 411) to 1.00 (Figures 5 and 6). The estimates showed high standard errors and tended to unity. Birth weight presented maternal correlations of 0.88; 0.84; 0.69; and 0.46 with weights at the ages of 85; 158; 231; and 411 days, respectively. These correlations among weights at 85 days and the weights at 158; 231; and 411 days were 1.00; 0.95; and 0.83, respectively. The weight at the age of 158 days showed maternal correlations of 0.96 and 0.85 with the weights at the ages of 231 and 411 days, respectively.

The random regression models used in this study allowed a reasonable adjustment of data and a more efficient use of available information. Functions with Legendre polynomials of fourth order were sufficient to adjust the random part, while the ordinary polynomials of third order (quadratic) were the best to adjust the fixed trajectory.

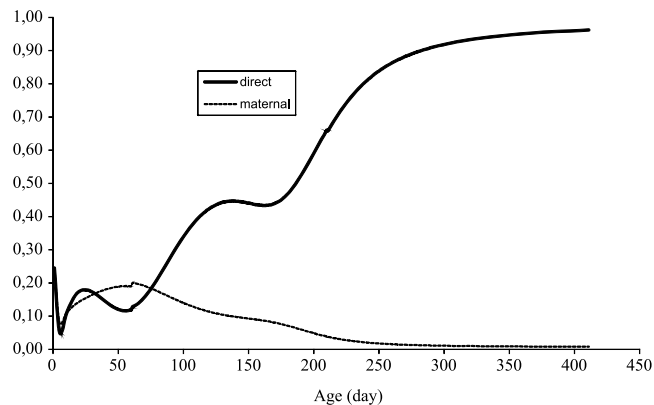


Figure 3 - Heritability estimates for direct and maternal effects estimated by random regression model with ordinary polynomials of third order (quadratic) in the fixed part and Legendre polynomials of fourth order (cubic) in the random part (model 6) for the Santa Inês breed, with weights taken from birth to 411 days of age.

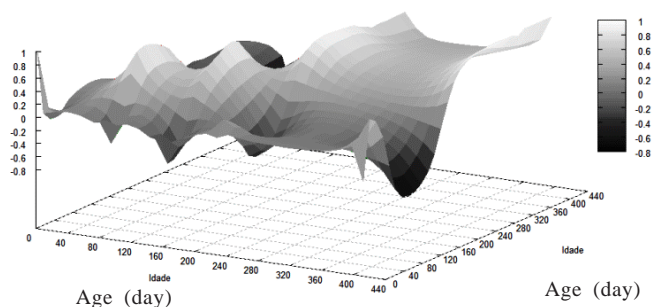


Figure 4 - Values of direct additive genetic correlation estimated by random regression model with ordinary polynomials of third order (quadratic) in the fixed part and Legendre polynomials of fourth order (cubic) in the random part (model 6), for the Santa Inês breed, with weights taken from birth to 411 days of age.

Fischer et al. (2004) used models with orthogonal polynomials (quadratic) in the fixed part with all combinations of Legendre polynomials of second and third order for the direct, maternal, individual permanent environmental and maternal permanent environmental effects on growth trajectory of the Poll Dorset breed. These authors found that the best adjustment occurred for the third-order model for direct and permanent environmental (individual and maternal) and second order for maternal effects. Fisher et al. (2006), also with the Poll Dorset breed, used quadratic Legendre polynomials for direct genetic and permanent environmental effects and linear polynomials for maternal effects. Lewis & Brotherstone (2002), in Suffolk breed, used orthogonal polynomials of order five (fourth) in the fixed part, varying the random part with Legendre polynomials from order three to five, and evaluating the presence or absence of maternal effect.

In Santa Inês breed, Sarmiento et al. (in press) evaluated the Legendre polynomials of order three (square) on the random trajectory and ranged these polynomials from two to eight in the fixed regression, maintaining a homogeneous residual variance. This author concluded that the use of a polynomial function of fourth order (cubic) was more

efficient to describe the average growth curve of the studied animals. It also should be emphasized the differences between the various studies, which reinforce the importance of evaluating different models for different data sets, regardless to the breed to be evaluated. It is also important to consider that the analysis should be performed jointly, with changes in estimates according to the combinations between the random and the fixed part. The best adjustment occurs for a better combination of factors because a given function evaluated at the fixed part may present different behavior according to the random function evaluated.

The standard estimates of additive genetic variance differed from that observed by Sarmiento et al. (in press). Mathematical functions tend to be adjusted to the observed points according to their dispersion in the available sample space. Thus, this author has studied the growth of this breed only up to 196 days of age, which may suggest the difference between his study and the present one. The same difference between the studies may be related to the maternal genetic variance.

Sarmiento et al. (2006a), evaluating the growth of sheep from Santa Inês breed, obtained growing direct heritabilities for weights from birth to 196 days of age ranging from 0.004 to 0.28. In the present study, considering the same period, direct heritabilities ranged from 0.05 to 0.56, with patterns of growth and decline, unlike that observed by Sarmiento et al. (2006a). For the maternal heritability, these authors reported an increase up to 56 days and then a decrease along the path. There was a reduction of maternal heritability estimates for the present study, from birth to approximately the fifth day, but a

Table 3 - Direct genetic (above diagonal) and phenotypic correlations (below diagonal) among the body weights of the Santa Inês breed taken at some selected ages between birth and 411 days old

	1	85	158	231	411
1	1.00	0.12	0.11	-0.18	-0.24
85	0.47	1.00	0.58	-0.56	-0.75
158	0.36	0.68	1.00	0.15	-0.29
231	0.09	-0.09	0.39	1.00	0.90
411	-0.03	-0.34	-0.11	0.85	1.00

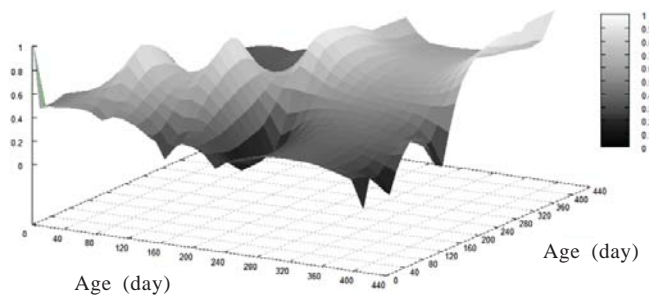


Figure 5 - Values of the phenotypic correlation estimated by random regression model with ordinary polynomials of third order (quadratic) in the fixed part and Legendre polynomials of fourth order (cubic) in the random part (model 6), for the Santa Inês breed, with weights taken from birth to 411 days old.

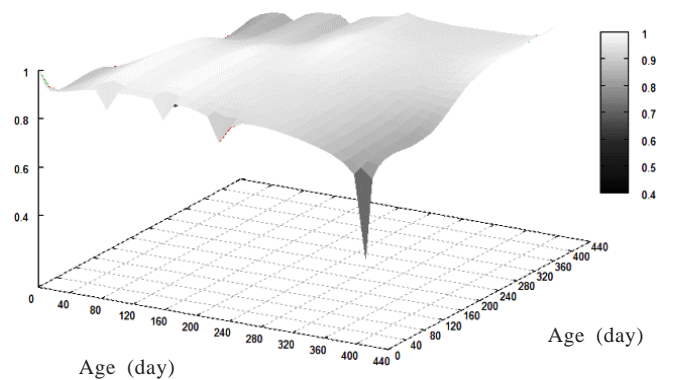


Figure 6 - Values for maternal additive genetic correlation estimated by random regression model with ordinary polynomials of third order (quadratic) in the fixed part and Legendre polynomials of fourth order (cubic) in the random part (model 6), for the Santa Inês breed, with weights taken from birth to 411 days of age

pattern similar to the study of Sarmiento et al. (2006a), from this day until 196 days of age was found.

Considering the weights at birth and weaning (around 50 days in herd), the direct heritabilities were 0.24 and 0.12, respectively. Estimates of maternal heritability for the same weights were 0.24 and 0.19, respectively. Lôbo (2002) reported for sheep averages for direct heritability of 0.33, 0.34 and 0.32 for birth weight, weight at 56 days and weaning weight, respectively. These values are higher than those observed in this study. Sousa et al. (1999), using an animal model for univariate analysis, estimated values of 0.13 and 0.04 for direct heritability and 0.12 and 0.10 for maternal heritability, respectively, for weights at birth and at 112 days of age (weaning). These values are lower than those observed in this study for the same breed. Sarmiento et al. (2006b) observed direct heritabilities of 0.20 and 0.00, respectively, for weights at birth and at weaning at 112 days old for Santa Inês breed. This value for birth weight is similar to that observed in this study.

Regarded to genetic correlations in this study, the results confirm what has been observed by other authors (Fischer et al., 2004, 2006; Lambe et al.; 2006; Sarmiento et al., in press), that genetic correlations among weights at subsequent ages, close together, are high, tending to unity and the weights at younger ages are not under the same genetic control than those taken in later life.

These aspects present a great importance to the process of animal selection. In studies that consider the weights taken at various ages as distinct traits and evaluated as repeated measures or longitudinal data, positive and high genetic correlations are usually observed between these weights, suggesting that early selection for a weight will promote genetic gains for the weights at older ages. However, most studies in which these traits are considered as infinite-dimensional characters, whose phenotype is described by a function, report distinct genetic controls between weights at early and late ages, often with negative genetic correlations, such as this study and that of Lambe et al. (2006). Therefore, we should consider this aspect to prevent that the early selection will be divergent from selection in later ages. It is known that the management conditions in the pre-weaning and post weaning are distinct, therefore two different environments are present. In order to increase the efficiency of selection of meat sheep, it should be further investigated if the fact that the best genotypes in the early stages of growth are not necessarily the same at the end of the trajectory might be a consequence of a possible genotype \times environment interaction.

Conclusions

Under the conditions of this study, we conclude that the random regression models are effective to adjust the growth curve of meat sheep. In these models, it is important that different functions must be evaluated with different orders of fit, both in the fixed as in random regression because the behavior of the trajectory may be different for each data set. The genetic variability observed in this population permit to change the trajectory of growth of the animals by selection. The genetic control of the weights in the early stages of growth is not the same that operates at older ages, which is important for the establishment of appropriate selection strategies. The selection of animals for slaughter at a young age should, therefore, be different from that for herd replacement animals.

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