OTÁVIO HENRIQUE GOMES BARBOSA DIAS DE SIQUEIRA

COMPARING NONLINEAR MIXED MODELS FOR GENETIC EVALUATION OF LACTATION CURVES IN DAIRY GOATS

Dissertation submitted to the Animal Science Graduate Program of the Universidade Federal de Viçosa, in partial fulfillment of the requirements for degree of *Magister Scientiae*.

VIÇOSA
MINAS GERAIS – BRASIL
2017

Ficha catalográfica preparada pela Biblioteca Central da Universidade Federal de Viçosa - Câmpus Viçosa

T

Siqueira, Otávio Henrique Gomes Barbosa Dias de, 1991-

S618c Comparing nonlinear mixed models for genetic evaluation
2017 of lactation curves in dairy goats / Otávio Henrique Gomes Barbosa Dias de Siqueira. – Viçosa, MG, 2017.

vi, 29f. : il. ; 29 cm.

Inclui apêndices.

Orientador: Fabyano Fonseca e Silva.

Dissertação (mestrado) - Universidade Federal de Viçosa.

Referências bibliográficas: f.12-15.

1. Caprinos. 2. Lactação. I. Universidade Federal de Viçosa. Departamento de Zootecnia. Programa de Pós-graduação em Zootecnia. II. Título.

CDD 22 ed. 636.39

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APPROVED: February, 23th, 2017.

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to all who made this moment possible
I dedicate

ACKNOWLEDGEMENTS

To God for my life, family and friends.

To my parents, for giving me life, for all my support in my journey to this day, for love and unconditional dedication.

To my supervisor Fabyano Fonseca e Silva for all the teachings conveyed, patience, opportunities he gave me and friendship.

To my co-supervisor Leonardo Siqueira Glória for his support, advice, teachings, and motivation to carry out this work.

I would like to thank the Universidade Federal de Viçosa and the Zootecnia Program for providing me the opportunity to carry out and conclude my Master, contributing to my academic and professional growth.

I thank my committee members, Moyés Nascimento and Camila Ferreira Azevedo, for their attention to this work, for spending their time on reading it and for their valuable suggestions.

I tank especially to Hinayah Rojas de Oliveira for making my days lighter, confusing and pleasant, for being present whenever I needed to spare my efforts, for all his fellowship.

I thank the team of the GRUMECA, for making this work possible, for all the time spent in collecting data, for friendship, and for making all the work lighter.

"***Clouds always change positions, but they are always clouds in the sky. So we must be every day, mutants, but loyal to what we think and dream; remember, everything falls apart in the air, only thoughts remain***"

(Paulo Beleki)

SUMMARY

ABSTRACT

SIQUEIRA, Otávio Henrique Gomes Barbosa Dias de, M.Sc., Universidade Federal de Viçosa, February, 2017. **Comparing nonlinear mixed models for genetic evaluation of lactation curves in dairy goats.** Adviser: Fabyano Fonseca e Silva. Co-adviser: Leonardo Siqueira Glória.

Knowledge on lactation curve is essential to validate the genetics, nutritional and reproductive adopted management, since it allows the evaluation of animals before the end of yielding, saving resources. By comparing the shape of curves among different groups of animals (genetic group, ages, herds and other treatments of interest), it is possible to access the effectiveness of the lactations, thus providing information for selection of the more productive groups. The study of lactation curves can be more attractive by using nonlinear mixed models since it is possible to make inferences when milk collections may be irregular in time; when there is incomplete group structure; when the adjacent evaluations are more closely correlated than the others; and when the response of individuals as a function of time has increasing variance. We aimed to fit and compare fifteen nonlinear mixed models to describe lactation curve of dairy goats as well as to estimate heritability and genetic correlations for the parameters of the selected model. The dataset was provided by the Caprine sector of the Universidade Federal de Viçosa. After checking the data consistency, we used 3,856 milk yield test-day records from 535 first lactations of Saanen and Alpine goats (including crosses). In order to identify the best nonlinear mixed model, different information criteria (AIC, AICc, AICu, BIC, cAIC and AIC3) were used here. Based on these criteria, the Wood model presented the best goodness of fit, being their parameters used as phenotypic observations for genetic evaluation of lactation curves. Additionally, the Wood model was integrated to calculate the total milk yield (TMY) that was also included in the genetic analysis. For this, a multi-trait mixed model was fitted by considering as traits the TMY and the a, b and c parameters of Wood model. The heritability estimates for TMY, a, b and c were 0.31, 0.17, 0.11 and 0,08, respectively. The genetic correlation between TMY and the parameters a, b and c were, 0.28, 0.22 and 0.17. Based on these results, the trait TMY can be indicated as selection criterion in dairy goats breeding programs, however the parameters of Wood model are not recommended to this aim.

RESUMO

SIQUEIRA, Otávio Henrique Gomes Barbosa Dias de, M.Sc., Universidade Federal de Viçosa, fevereiro de 2017. **Comparação de modelos não lineares mistos para análise de curva de lactação em caprinos leiteiros.** Orientador: Fabyano Fonseca e Silva. Coorientador: Leonardo Siqueira Glória.

O conhecimento sobre a curva de lactação é essencial para validar o manejo genético, nutricional e reprodutiva adotada, por permitir a avaliação de animais precocemente, gerando economia. Ao comparar a forma das curvas entre diferentes grupos de animais (grupo genético, idades, rebanhos), é possível avaliar a eficácia das lactações, proporcionando informações para a seleção dos grupos mais produtivos. Torna-se mais interessante o estudo das curvas de lactação ao usar modelos mistos não lineares, pois é possível fazer inferências mesmo com coletas de leite irregulares; quando há estrutura de grupo incompleta; quando as avaliações adjacentes estão mais correlacionadas do que as demais; e quando a resposta dos indivíduos em função do tempo tem variação crescente. Pretedeu-se ajustar e comparar modelos não lineares mistos para descrever a curva de lactação de cabras leiteiras, bem como estimar herdabilidade e correlações genéticas para os parâmetros do modelo selecionado. Os dados são do setor caprinos da Universidade Federal de Viçosa, após verificar a consistência dos dados, utilizou-se 3.856 registros de produção de leite das 535 primeiras lactações de Saanen e cabras alpinas (incluindo cruzados). Para identificar o melhor modelo, utilizou-se diferentes critérios de informação (AIC, AICc, AICu, BIC, cAIC e AIC3). Com base nos critérios, o modelo de Wood apresentou a melhor qualidade de ajuste, sendo seus parâmetros utilizados como observações fenotípicas para avaliação genética de curvas de lactação. Além disso, o modelo de Wood foi integrado para calcular a produção total do leite (TMY) que também foi incluído na análise genética. Para isso, um modelo misto multicaracterístico foi ajustado ao considerar como características a produção total e os parâmetros a, b e c do modelo de Wood. As estimativas de herdabilidade para TMY, a, b e c foram 0,31, 0,17, 0,11 e 0,08, respectivamente. A correlação genética entre TMY e os parâmetros a, b e c foram 0,28, 0,22 e 0,17. Com base nesses resultados, a característica TMY pode ser critério de seleção porém, os parâmetros do modelo de Wood não são recomendados para este fim.

INTRODUCTION

1. GOAT MILK AND LACTATION CURVES

The goat milk is classified like functional food, because assists it in maintaining human health with beneficial effects on physiological functions. This milk is high digestibility and it is considered less allergenic than cow's milk. Furthermore, it presents higher content of calcium, phosphorus and potassium (Godoi e Portilho, 2009), higher digestibility of the lipid fraction, and the lower content of cholesterol (Silva et al., 2013). Some studies indicated that goat milk fat is more efficient used in human feeding than cow milk fat (Alferez et al., 2001).

To produce a quality and a large volume milk, some factors must be taken into account such as genetics, lactation order, breed, age and nutrition (Morand-Fehr, 2005). It must be emphasized that among the insoluble milk constituents, we highlight the levels of protein and fat, as they have great importance for dairy industry (Oliveira et al., 2015). In this context, it is essential to understand the effects of the mentioned factors on milk, protein and fat across time under a lactation curve approach

Knowledge on lactation curve is essential to validate the genetics, nutritional and reproductive adopted management, since it allows, the evaluation of animals before the end of yielding, saving time and financial resources. By comparing the shape of curves among different groups of animals (genetic group, ages, herds and other treatments of interest) it is possible to access the effectiveness of the lactations, thus providing information for selection of the more productive groups. The use of empirical mathematical models has allowed to study the lactation curves of domestic animals (Wood,1967,Leon-Velarde et al., 1995). In general, the shape of a typical lactation curve may be described as increasing, at a relatively high rate, up to the point where peak production is obtained, after which it declines at a slower rate until the end of milk production (González-Peña,2012).

The utility of the lactation models depends on the model efficiency to describe the biological process (Olori et al.,1999). Since a given model is validated, it can be used in breeding programs to improve the economic and biological efficiency of the herd and the total milk yield estimation (El Faro, 1996).

2. NONLINEAR MIXED MODELS

Nonlinear models allow to study complex biological process such as lactation curves. In summary, a model is classified as nonlinear if at least one of the partial derivatives of the nonlinear function in relation to the parameters depends on at least one of the parameters of the model. These models generally deduced from theoretical assumptions and the resulting parameters are interpretable under biological viewpoint.

Nonlinear models can be defined as follows:

$$y_i = f(x_i, \theta) + \varepsilon_i, i = 1, \dots, n$$

Where:

y_i represents the observation of the dependent variable (*i* = 1,2,…,*n*);

$f(x_i, \theta)$ is the expected function;

x_i represents the observation of the independent variable;

$\theta = [\theta_1, \theta_2, \dots, \theta_p]'$ is an unknown p-dimensional parameter vector;

ε_i represents the assumed unobservable random error effect, with mean zero and unknown variance σ^2.

Nonlinear regression models are suitable for analyzing data for which there is an empirical or theoretically functional relationship between the dependent and independent variables. Lactation and growth curves are widely studied by using these models (Gloria, 2014). Typically, the fitting of nonlinear models is done through the ordinary least squares method via an iterative process. This iterative process proceeds until some criterion adopted for convergence is achieved.

The nonlinear mixed models can be considered an extension of nonlinear regression models by assuming random and fixed effects affecting the parameters of interest (Bates and Watts, 1988).For example, suppose that the experimental data are in the form of repeated measurements on the response and explanatory variables of various subjects, and the aim is to fit a model that represents simultaneously the overall nonlinear global structure as well as the variability between and within of subjects. This situation requires a nonlinear mixed model (Glória,2014). Random effects are used to represent dependence within groups of animals.

The nonlinear mixed models can be represented as follows:

$$y_{ij} = f(\phi_{ij}, v_{ij}) + \epsilon_{ij}, i = 1, \ldots, M, j = 1, \ldots, n_i,$$

Where: M is the number of groups, n_i is the number of observations on the group *I*, f is a general function, differentiable of a specific group of vector parameters ϕ_{ij} and a covariate vector v_{ij}, and ϵ_{ij} is a normal distribution within the error-group term. The model of the vector ϕ_{ij}, is:

$$\phi_{ij} = A_{ij}\beta + B_{ij}b_i, b_i \sim N(0, \psi),$$

Being β a p-dimensional vector of fixed effects and b_i is a vector of random effects with dimension q associated with group i (not varying with j) with variance-covariance matrix ψ. The matrices A_{ij} and B_{ij} depend on the group and the values of covariates in the *j*th observation. This model is a generalization described by Lindstrom and Bates (1990), where A_{ij} and B_{ij} may depend on$j$. Assume that the observations are independent, the residuals ϵ_{ij} are distributed as $N(0, \sigma^2)$.

The study of lactation curves can be more attractive when using nonlinear mixed models since it is possible to consider the following features: a) Milk collections may be irregular in time, i.e. the interval between any two consecutive measurements is not necessarily equidistant; B) have an incomplete group structure; C) the adjacent evaluations are more closely correlated than the others; and D) the response of individuals as a function of time has increasing variance.

3. GENETIC PARAMETERS

Heritability can be defined as the fraction of total variation between animals for a given trait, which is due to genes and therefore passed from parents to offspring. It can range from 0 to 1, and high values mean that the genetic differences found between the individuals are responsible for the variation of the trait, whereas low values imply that much of the variation is due to environmental differences. When the heritability of a trait is high, the correlation between the genetic value and the phenotype is also, and the phenotypic value of the animal can be a good indication of the genetic value of the animal. In general the levels of heritability can be defined as follows: high heritability from values higher them 0.4, the middle heritability of 0.2 to 0.4, and low heritability to 0 at 0.2.

In dairy livestock traits such as milk production, fat production and protein production presents middle-high heritability (around 0.3), and traits as percent of protein and fat percent presents high heritability. The low heritability usually is associated with reproductive traits

In this way, knowing the heritability of the trait is essential for breeding programs and fundamental for the prediction of the genetic value of the animals. Thus, the heritability to be calculated by:

$$h^2 = \frac{\sigma_g^2}{\sigma_p^2},$$

where:

σ_g^2 is the estimate of the additive genetic variance;

σ_p^2 is the estimate of the phenotypic variance.

Knowledge of the correlation between traits is of great importance for breeding programs, since traits with favorable correlations can be improved indirectly even if they are not the target of selection, but they can also affect selection if they have an unfavorable correlation. When considering milk production traits, the favorable correlation can be exemplified by the correlation between lactation peak and total milk yield, how higher the lactation peak, higher will be the total milk yield.

Thus, the knowledge of the correlations is another tool used in the selection that can reduce costs, since if the trait of interest, for example, is expressed late, but another trait that has high and favorable correlation expresses itself early, the selection can be made by this feature, which reduces the expense of keeping non-indicated animals for a long time.

The genetic correlation can be calculated by:

$$\frac{COV(x,y)}{\sqrt{\sigma_x^2 * \sigma_y^2}},$$

where: COV (x, y) is the genetic covariance between the trait of interest (x, y); σ_x^2 is the genetic variance of trait x and σ_y^2 is the genetic variance of trait y.

MATERIALS AND METHODS

1. DATA DESCRIPTION

After checking the data consistency, we used 3,856 milk yield (MY) , fat percentage (FP), and protein percentage (PP) test-day records from 535 first lactations of Saanen and Alpine goats (including crosses) belonging to Universidade Federal de Viçosa, Brazil. The relationship matrix included a total of 1,061 animals, up to 3 previous generations for animals with phenotypic data.

The goats were kept in collective stalls under the free-stall system and received feed composed of corn silage and hay, in addition to a concentrated mixture, provided according to their nutritional requirements. The goats kidded between 2000 and 2014, and the MY records were obtained by mechanical milking. Milk components were estimated using the infrared analysis equipment MilkoScan Minor (Foss, Hillerød, Denmark) at the Milk Quality Laboratory of the Universidade Federal de Viçosa.

The MY, FP, and PP records were measured weekly, varying from 1 (starting subsequently on the fifth day after kidding) to 40 wk. According to Meyer (2005), random regression models using polynomials of high orders require that each animal has more records than the order of the polynomials to avoid implausible (co) variance component estimates. Thus, only animals with at least 5 records were included in the analyses. Data considered as outliers (μ ± 3 standard deviation (SD), inside the contemporary group) were discarded.

Contemporary groups were defined by the combination of year and season of kidding, litter size (1 or 2 kids), and breed composition (Alpine ≥ 90%, Saanen ≥ 90%, and crossbreed between Alpine and Saanen goats, with 172, 122, and 241 animals, respectively), with the restriction that each group had to contain at least 5 animals. The age of the dam at kidding was included as a covariate with a linear effect for all traits. Trait means and SD for MY, FP, and PP were, respectively, 2.33 kg (0.96), 4.51% (0.86), and 4.09% (0.38).

2. STATISTICAL ANALYSES

Statistical analyses where performed using two independents steps. Firstly, the nonlinear functions (Table 1) were used to describe lactation curves trough maximum likelihood method by means of nlme (Nonlinear Mixed-Effects Model) package of R software (R Core Team, 2013)

Table 1. Nonlinear functions fitted to lactation curve data of dairy goat.

Equation	Function
Ratio of polynomials	$Y_t = t / (a + bt + ct^2)$
Gaines or Brody	$Y_t = ae^{-ct}$
Sikka	$Y_t = ae^{(bt-ct^2)}$
Cobby and Le Du	$Y_t = a(1-e^{-ct}) - bt$
Wilmink	$Y_t = a + be^{-kt} + ct$
Dijkstra	$Y_t = aexp\left[\frac{b}{c}(1-e^{-ct}) - dt\right]$
Wood	$Y_t = at^b e^{-ct}$
Jenkins and Ferrell	$Y_t = at e^{-ct}$

In general, the lactation curve parameters (Table 1) may be interpreted as follow (Varona,1998): a time-dependent variable (t), initial yield (a), ascent to peak (b), and descent from peak (c). Functions of these parameters describe characteristics of the lactation curve, including initial yield, peak yield and time of peak yield (Gipson, 1989).

In all functions presented in table 1, the parameters were decomposed into a fixed and random effects. For example, considers the wood model:

$$Y_t = (\mu_a + GC_a + \varepsilon_a) * t^{(\mu_b + GC_b + \varepsilon_b)} exp(-(\mu_c + GC_c + \varepsilon_c)t) + \varepsilon_t$$

where:

Y_t is the production on the time *t,* μ_a, μ_b, μ_c are the general mean for each parameter, GC_a, GC_b, GC_c, are the fixed effects of contemporary group for each parameter, and ε the random effect associated for each parameter. The ε term was added for all parameters because believing the additive genetic can be present ε_t was the error associated. In order to determine the nonlinear model that best fitted to the lactation curve data of the studied goat population, the following goodness of fit measures were used: AIC, Akaike`s Information Criterion, (Akaike, 1974), AICc, corrected Akaike criterion (Sugiura, 1978; Hurvich and Tsai, 1989), Aicu, (McQuarrie,1997), BIC Bayesian Information Criterion (Schwarz, 1978), Caic and AIC_3 (Bozdogan, 1987).

In the table 2, the terms l, k and n represents, respectively, the maximum of the natural logarithm of the likelihood function of the model with the parameters, number of parameters, is the number of observations.

Table 2 - Different information criterion used to compare the fitted nonlinear mixed model.

CRITERION	FORMULA
AIC	$-2l + 2k$
AIC_c	$-2l + 2k + \frac{2k(k+1)}{n-k-1}$
AIC_u	$-2l + 2k + \frac{2k(k+1)}{n-k-1} + n * log\left(\frac{n}{n-k-1}\right)$
AIC_3	$-2l + 3k$
BIC	$-2l + 2klog(n)$
CAIC	$-2l + k * log(n)$

After choosing the best model the total milk yield was calculated though interception of the selected function.

In the second step, the genetic analyses where performed for all four traits (parameters estimate) using a multiple trait mixed model given by:

,**Y= Xβ + Zu + e** (1)

where: **Y** represents the vector of observations from the three phenotypes (a, b and c estimates and TMY) for each animal; **β** is the vector of fixed effects for the trait (the mean); **u** is the vector of random animal effects, $\mathbf{u} \sim \mathrm{N}(\mathbf{0}, \Sigma_{\mathrm{u}} \otimes \mathbf{A})$, being **A** the additive pedigree based relationship matrix, and **e** represents the residual vector, $\mathbf{e} \sim \mathrm{N}(\mathbf{0}, \Sigma_{\mathrm{e}} \otimes \mathbf{I})$. The matrices **X** and **Z** represent the incidence matrices for **β** and **u**, respectively. This model, allows to estimate the heritabilities and genetic correlations by using the estimates of the genetic and residual covariance matrices ($\hat{\Sigma}_{\mathrm{u}}$ and $\hat{\Sigma}_{\mathrm{e}}$), as well as the prediction of genetic breeding values (**û**).

In general terms, the model presented in (1) can be rewriting as follow:

$$\begin{bmatrix} Y_a \\ Y_b \\ Y_c \\ Y_{TMY} \end{bmatrix} = \begin{bmatrix} X_a & 0 & 0 & 0 \\ 0 & X_b & 0 & 0 \\ 0 & 0 & X_c & 0 \\ 0 & 0 & 0 & X_{TMY} \end{bmatrix} \begin{bmatrix} b_a \\ b_b \\ b_c \\ b_{TMY} \end{bmatrix} + \begin{bmatrix} Z_a & 0 & 0 & 0 \\ 0 & Z_b & 0 & 0 \\ 0 & 0 & Z_c & 0 \\ 0 & 0 & 0 & Z_{TMY} \end{bmatrix} \begin{bmatrix} u_a \\ u_b \\ u_c \\ u_{TMY} \end{bmatrix} + \begin{bmatrix} e_a \\ e_b \\ e_c \\ e_{TMY} \end{bmatrix},$$

where:

X and **Z** are incidence matrices relating records of the TMY, a, b and c parameters to fixed and random animal effects, respectively.

RESULTS

1. COMPARING NONLINEAR MIXED MODELS

All models were successfully fitted to lactation curve data. It is important to emphasize that the criterion for convergence and the number of iterations were the same for all models.

The goodness of fit analysis used to reveal the most appropriate model to describe the lactation curve in dairy goats is presented at Table 3.

Table 3 - Goodness of fit for lactation models trough different criteria.

Model	Information Criterion					
	AIC	AIC_c	AIC_u	AIC_3	BIC	CAIC
Ratio of polynomials	9335.7	9082.9	9394.1	11498.4	11200.4	9633.7
Gaines or Brody	8254.3	8074.9	8280.3	9698.5	9499.5	8453.3
Sikka	8006.2	7753.4	8064.6	10168.9	9870.9	8304.2
Cobby and Le Du	11593.9	11342.5	11651.6	13742.1	13446.1	11889.9
Wilmink	8108.5	7855.7	8166.9	10271.2	9973.2	8406.5
Dijkstra	8008.9	7694.7	8111.4	10868.3	10474.3	8402.9
Wood	7891.8	7639.1	7950.3	10054.5	9756.5	8189.8
Jenkins and Ferrell	9883.8	9704.5	9909.8	11328.0	11129.0	10082.8

According to Table 3, the Wood model presented the lowest AIC, AICc, AICu, AIC3, BIC and CAIC, thus it was chosen as the most appropriate to describe the lactation curve of dairy goats analyzed in this study. On the other hand, the Cobby and Le Du model was the worse one to describe these data.

2. GENETIC ANALYSIS OF LACTATION CURVES

With the choice of the best model, Wood model, the genetic analyzes were performed, to obtain the heritabilities and correlations.

The genetic parameter estimates of wood model given by heritabilities and correlations are shown in Tables 4. The heritability of initial yield was median (0.17) and its correlation with the total milk yield was 0.28. The genetic correlation between parameters estimates and total milk yield was lower for the parameters b and c (0.22 and –0.17, respectively).

Table 4 - Heritability (diagonal) and genetic correlations for the parameters of Wood model a is the initial milk yield; b is the ascent to peak; c is the descent from peak; and TMY is the total milk yield adjusted to 285 days.

	Parameters			
	A	b	C	TMY
a	0.1789	0.1553	-0.1038	0.2896
b	0.1553	0.1165	-0.0978	0.2270
c	-0.1038	-0.0978	0.0803	-0.1701
TMY	0.2896	0.2270	-0.1701	0.3143

DISCUSSION

1. COMPARING NONLINEAR MIXED MODELS

The use of a nonlinear mixed models is required her to describe lactation curves with a reasonable degree of interpretability and parsimony. The parameters of the models compared in this study (Table 3) allow to make inferences that are of interest to animal scientists, such initial yield, total milk yield, persistency of lactation and lactation peak, among other. The comparison of the models via information criteria are bored on the parsimony principle that relates to the number of parameters that are included in a nonlinear model built to mimic reality (in this case, the lactation curve).

The models compared in Table 3 contain information concerning the fixed effects that may influence the nonlinear (population) parameters and concerning the random factors that ultimately alter the shape of the predictand trajectory because of individual effects and possible correlations among records collected for the same individuals. Since Wood model presented the best fit quality based on the used information criteria, we expected this model reflects all mentioned characteristics and be useful to be exploited under genetic valuation approach.

Williams (1993) evaluated the quality of fits of nonlinear and linear models fit to the lactation curve of white British dairy goats and they concluded that Morant linear was the best model, different of the results of Fernadéz (2002) that indicates the Gipson and Grossman models, different too the we study when the best model was the Wood model (Portolano,1997, Ruvuna, 1997, Jacopini,2013). The different of best models to fit the lactation curve of dairy goats may can be explained because the different used breed.

2. GENETIC ANALYSIS OF LACTATION CURVE

With the selection of the model, the estimation of the genetic parameters was performed and the heritabilities and correlations was show in table 4. The heritability of parameter a was median (0.17) and its correlation with TMY (was equal to 0.28). The genetic correlation between TMY with the parameters b and c was lower 0.22 and –0.17, respectively. The genetic correlation between parameters a and b was lower too (-0.09). The correlation between a and c (-0.1) possibly because of the intensive feeding of high yielding goats, which led to greater performance during the initial days of lactation. Goats with higher initial yield have a faster descent from peak. Finally, the heritability for the second parameter (0.11) was considerably smaller than the heritabilities obtained for the third parameter (0.08) and for total milk yield (0.31). Our estimates were similar to those obtained in previous studies for heritability to TMY (Analla,1996; Kala, 1990; Boichard 2, 1989). However, the heritability to the parameters of Wood model are scarce for dairy goats, but we result are consistent with orders ruminants.

The genetic structure of the correlations among parameters of the yield function (a, b, and c) and TMY indicates that selection for a 285-d milk yield involves an increment in the initial milk yield (a) a little increment in ascent to peak (b) and a little decrease of descent from peak (c).

CONCLUSION

In general, the selection will be more efficient to TMY then order parameters, but the selection based on “a” parameters, initial yield can be realized previously and is correlated to the others traits even then was a low correlation, but the increased of this trait will improve the rest, thus being another tool to the breeding programs.

So, based on these results, the trait TMY can be indicated as selection criterion in dairy goats breeding programs, however the parameters of Wood model are not recommended to this aim.

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APPENDIX A

R CODES TO FIT NONLINEAR MIXED MODELS

```
##### Identificando local dos dados####################################

setwd("C:\\Users\\InforCenter\\Desktop\\UFV\\Mestrado\\Tese\\Análises\\Dados")

####################Entrando com os dados#################

dados <- read.table("Dados.txt", h = T)

require(nlme)

dadosg=groupedData(PLDC~Semana|Animal,dados)
head(dadosg)

dadosg$GC=factor(paste0(dadosg$NC,dadosg$GG, dadosg$AnoEst))

L=c();K=c();nm=c()
aic=c();aicc=c();aicu=c();caic=c();bic=c();aic3=c()


############wood###########################

modelWood=nlme(PLDC~a*(Semana**b)*exp(-
C*Semana),fixed=list(a+b+C~1),random=pdDiag(a+b+C~1),control=nlmeControl(
minScale=10**-100,maxIter=100000),data=dadosg,start=list(fixed
=c(0.5,0.5,0.003)),na.action=na.omit)

modelWood=nlme(PLDC~a*(Semana**b)*exp(-C*Semana),fixed=list(a~GC-
1,b~GC-1,C~GC-
1),random=pdDiag(a+b+C~1),control=nlmeControl(minScale=10**-
100,maxIter=100000),data=dadosg,

start=list(fixed=c(1.68E+00,2.46E+00,2.594852,2.2284421,1.2223298,0.139477,0.
9921046,1.76925394,1.3588812,1.373766,1.813947,1.1746926,1.7435309,2.814
9,2.5959962,1.681322729,2.4097798,2.76883,3.328374,0.396069,1.8451649,0.1
22914,0.591741,1.0531133,1.8687831,0.9224393,1.4167372,1.65712323,1.3449
831,2.94533,1.8292696,0.327588,2.3546712,1.035632,2.421113,0.550032,2.046
6555,2.829357,1.681466378,1.8719758,499.988177,1.169055,1.7932174,1.5196
004,1.71718185,1.929646,2.1380686,14.357807,1.1662302,1.67795754,1.67861
7415,2.6337883,3.050674,2.3195633,1.8307679,0.83895,1.8895659,0.8203222,2
.0163059,4.940018,1.9486681,2.6724184,2.825976,3.059664,1.2161905,1.70523
515,2.779399,2.921934,0.6378,1.70238884,1.3065785,1.64075493,1.8956444,1.
67316174,1.884706,1.5702855,3.450501,2.960194,2.0774135,1.9502059,1.6456
9342,3.203651,1.2473571,1.678277548,2.4328635,1.6608602,1.8355315,4.1591
69,0.9994388,2.2423041,1.9265005,1.1909925,1.5184524,1.5604031,3.097094,1
.66170279,3.107582,0.725443,0.3780585,0.2717646,0.36255296,0.33107024,0.4
7668059,1.240376,0.5805917,0.4803384,0.5649496,0.6039333,0.35519133,0.52
06736,0.41784845,0.3032968,0.1200088,0.39671458,0.33717028,-0.1542595,-
```

```
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606,0.34248854,0.0221403,0.1374132,1.237772,0.1705966,1.0058148,0.242935
9,0.8737451,0.2612479,0.1989316,0.4770719,0.0201168,-2.4249035, 0.5012035,
0.45137853, 0.45473711,0.387571565,0.564766,0.5327184,-1.0556825,
0.7012105,
0.6438749,0.43589137,0.0815651,0.1581453,0.0891632,0.5036888,0.466245,0.4
0098086,1.1781989,0.30075222,-0.4637346,0.3053304,-0.0159086, 0.33482757,
0.2183728,0.6182521,0.6076465,0.1173754,0.35508926,1.4530235,0.31233074,
0.7008309,0.382875291,0.42639371,0.28420136,0.378547985,0.40130211,0.223
3571,0.0323069,0.2459386,0.47752685,-0.2702767, 0.1321608, 0.44429196,
0.384197473, 0.2685028, 0.5072514,0.32679849,-0.8503375, 0.42831328,
0.178492,0.28693079,0.6178201,0.2185799,0.2396411,0.1507727,0.4832558,-
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925,0.0604544,0.039894477,0.044593876,0.0504054,0.06324296,0.035052829,0
.041730751,0.045240684,0.049891274,0.031649188,0.042872061,0.046723489,-
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0.01831528, 0.07106218, 0.043369492,0.040142684,0.14645505,0.02727197,-
0.02019026,
0.035568667,0.00687975,0.05796689,0.05126585,0.045782736,0.05702668,0.01
242205,0.05067098,0.1235809,0.02116033,0.0873154,0.05857209,0.0719001,0.
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044314,-0.02195324, 0.042135597,0.040016058, 0.032184862,0.042791284,
0.05700609,0.043988056,-0.03832356, 0.014714,  0.049425563, 0.02451466,
0.044188023,0.01676766,0.01479717,0.042871012,0.04880787,0.01412836,0.07
574051)),na.action=na.omit)

L[1]=modelWood$logLik
K[1]=attributes(logLik(modelWood))$df
nm[1]=nrow(dadosg)
aic[1]=-2*L[1]+2*K[1]
aicc[1]=aic[1]+((2*K[1]*(K[1]+1)/nm[1]-K[1]-1))
aicu[1]=aicc[1]+nm[1]*log(nm[1]/(nm[1]-K[1]-1))
caic[1]=-2*L[1]+K[1]*(1+log(nm[1]))
bic[1]=-2*L[1]+K[1]*log(nm[1])
aic3[1]=-2*L[1]+3*K[1]


##############################Jenkins########################


            modelJenkins=nlme(PLDC~a*Semana*exp(-
C*Semana),fixed=list(a+C~1),random=pdDiag(a+c~1),control=nlmeControl(minSc
ale=10**-100,maxIter=100000),data=dadosg,start=list(fixed
=c(0.5,0.003)),na.action=na.omit)
```

```
            modelJenkins=nlme(PLDC~a*Semana*exp(-
C*Semana),fixed=list(a~GC-1,C~GC-
1),random=pdDiag(a+C~1),control=nlmeControl(minScale=10**-
100,maxIter=100000),data=dadosg,
                        start=list(fixed
=c(0.662179,0.662179,0.662179,0.662179,0.662179,0.662179,0.662179,0.66217
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868,0.08067868,0.08067868,0.08067868,0.08067868,0.08067868,0.08067868,0.
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868,0.08067868,0.08067868,0.08067868,0.08067868,0.08067868,0.08067868,0.
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08067868,0.08067868,0.08067868,0.08067868,0.08067868,0.08067868,0.08067
868)),na.action=na.omit)

L[3]=modelJenkins$logLik
K[3]=attributes(logLik(modelJenkins))$df
nm[3]=nrow(dadosg)
aic[3]=-2*L[3]+2*K[3]
aicc[3]=aic[3]+((2*K[3]*(K[3]+1)/nm[3]-K[3]-1))
aicu[3]=aicc[3]+nm[3]*log(nm[3]/(nm[3]-K[3]-1))
caic[3]=-2*L[3]+K[3]*(1+log(nm[3]))
bic[3]=-2*L[3]+K[3]*log(nm[3])
aic3[3]=-2*L[3]+3*K[3]

####Ratio####################
```

```
modelRatio=nlme(PLDC~(a*(Semana+b))/(Semana+b)^2+(C^2),fixed=list(a+b+C~
1),random=pdDiag(a+b+C~1),control=nlmeControl(minScale=10**-
100,maxIter=100000,tolerance = 0.001),data=dadosg,start=list(fixed
=c(0.5,0.5,0.003)),na.action=na.omit)
```

```
modelRatio=nlme(PLDC~(a*(Semana+b))/(Semana+b)^2+(C^2),fixed=list(a~GC-
1,b~GC-1,C~GC-
1),random=pdDiag(a+b+C~1),control=nlmeControl(minScale=10**-
100,maxIter=100000,tolerance = 0.001),data=dadosg,start=list(fixed =c(-
1.596700306,-0.896457293,-0.092961835,-0.190553619,-0.463060242,-
1.923592396,0.735610899,-0.090203288,-0.083679806,-
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13.36226671, -13.36226672       , -13.36226673       ,-13.36226674,
```

```
1.478573223,1.600185964, 1.666791676,1.573186288, 1.382661715,
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,1.4711231,1.549710921,1.589236634,1.446381404,1.479661171,1.591758465,1
.54587556,1.702788319,1.377887964,1.732322378,1.122702203,1.475828446,1.
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605734196,1.567962215,1.609856224,1.53210558,0.880049643,1.577868536,1.
261861461,1.607856675,1.622989024,1.401281947,1.54337877,1.447141814,1.
579787906,1.468407819,1.355500049)),na.action=na.omit)

L[4]=modelRatio$logLik
K[4]=attributes(logLik(modelRatio))$df
nm[4]=nrow(dadosg)
aic[4]=-2*L[4]+2*K[4]
aicc[4]=aic[4]+((2*K[4]*(K[4]+1)/nm[4]-K[4]-1))
aicu[4]=aicc[4]+nm[4]*log(nm[4]/(nm[4]-K[4]-1))
caic[4]=-2*L[4]+K[4]*(1+log(nm[4]))
bic[4]=-2*L[4]+K[4]*log(nm[4])
aic3[4]=-2*L[4]+3*K[4]

#########################Gaines or Brody###############

modelGaines=nlme(PLDC~a*exp(-
C*Semana),fixed=list(a+C~1),random=pdDiag(a+C~1),control=nlmeControl(minSc
ale=10**-100,maxIter=100000),data=dadosg,start=list(fixed
=c(0.5,0.003)),na.action=na.omit)

modelGaines=nlme(PLDC~a*exp(-C*Semana),fixed=list(a~GC-1,C~GC-
1),random=pdDiag(a+C~1),control=nlmeControl(minScale=10**-
100,maxIter=100000),data=dadosg,start=list(fixed=c(2.91167052,2.91167052,2.91
167052,2.91167052,2.91167052,2.91167052,2.91167052,2.91167052,2.9116705
2,2.91167052,2.91167052,2.91167052,2.91167052,2.91167052,2.91167052,2.91
167052,2.91167052,2.91167052,2.91167052,2.91167052,2.91167052,2.9116705
2,2.91167052,2.91167052,2.91167052,2.91167052,2.91167052,2.91167052,2.91
167052,2.91167052,2.91167052,2.91167052,2.91167052,2.91167052,2.9116705
2,2.91167052,2.91167052,2.91167052,2.91167052,2.91167052,2.91167052,2.91
167052,2.91167052,2.91167052,2.91167052,2.91167052,2.91167052,2.9116705
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167052,2.91167052,2.91167052,2.91167052,2.91167052,2.91167052,2.9116705
2,2.91167052,2.91167052,2.91167052,2.91167052,2.91167052,2.91167052,2.91
167052,2.91167052,2.91167052,2.91167052,2.91167052,2.91167052,2.9116705
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167052,2.91167052,2.91167052,2.91167052,2.91167052,0.01251059,
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01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251
059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.
01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251
059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.
01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251
059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.
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059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.
01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251
059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.01251059,0.
01251059,0.01251059)),na.action=na.omit)

L[8]=modelGaines$logLik
K[8]=attributes(logLik(modelGaines))$df
nm[8]=nrow(dadosg)
aic[8]=-2*L[8]+2*K[8]
aicc[8]=aic[8]+((2*K[8]*(K[8]+1)/nm[8]-K[8]-1))
aicu[8]=aicc[8]+nm[8]*log(nm[8]/(nm[8]-K[8]-1))
caic[8]=-2*L[8]+K[8]*(1+log(nm[8]))
bic[8]=-2*L[8]+K[8]*log(nm[8])
aic3[8]=-2*L[8]+3*K[8]

###############################Sikka############################

modelSikka=nlme(PLDC~a*exp((b*Semana)-
(C*(Semana*Semana))),fixed=list(a+b+C~1),random=pdDiag(a+b+C~1),control=nl
meControl(minScale=10**-100,maxIter=100000),data=dadosg,start=list(fixed
=c(0.5,0.3,0.003)),na.action=na.omit)

modelSikka=nlme(PLDC~a*exp((b*Semana)-
(C*(Semana*Semana))),fixed=list(a~GC-1,b~GC-1,C~GC-
1),random=pdDiag(a+b+C~1),control=nlmeControl(minScale=10**-
100,maxIter=100000),data=dadosg, start=list(fixed
=c(2.718925244,2.718925244,2.718925244,2.718925244,2.718925244,2.718925
244,2.718925244,2.718925244,2.718925244,2.718925244,2.718925244,2.71892
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25244,2.718925244,2.718925244,2.718925244,2.718925244,2.718925244,2.718
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18,0.000454218,0.000454218,0.000454218,0.000454218,0.000454218,0.000454
218,0.000454218,0.000454218,0.000454218,0.000454218)),na.action=na.omit)

L[10]=modelSikka$logLik
K[10]=attributes(logLik(modelSikka))$df
nm[10]=nrow(dadosg)
aic[10]=-2*L[10]+2*K[10]
aicc[10]=aic[10]+((2*K[10]*(K[10]+1)/nm[10]-K[10]-1))
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aicu[10]=aicc[10]+nm[10]*log(nm[10]/(nm[10]-K[10]-1))
caic[10]=-2*L[10]+K[10]*(1+log(nm[10]))
bic[10]=-2*L[10]+K[10]*log(nm[10])
aic3[10]=-2*L[10]+3*K[10]


################Cobby & Le Du#############################
modelCobby2=nlme(PLDC~a*(1-exp(-C*Semana))-
b*Semana,fixed=list(a+b+C~1),random=pdDiag(a~1),control=nlmeControl(minScal
e=10**-100,maxIter=100000),data=dadosg,start=list(fixed
=c(3.13381849,0.04132488,1.10599413)),na.action=na.omit)

modelCobby2=nlme(PLDC~a*(1-exp(-C*Semana))-b*Semana,fixed=list(a~GC-
1,b~GC-1,C~GC-1),random=pdDiag(a~1),control=nlmeControl(minScale=10**-
100,maxIter=100000,tolerance=0.001),data=dadosg,
             start=list(fixed
=c(3.13381849,3.13381849,3.13381849,3.13381849,3.13381849,3.13381849,3.1
3381849,3.13381849,3.13381849,3.13381849,3.13381849,3.13381849,3.133818
49,3.13381849,3.13381849,3.13381849,3.13381849,3.13381849,3.13381849,3.1
3381849,3.13381849,3.13381849,3.13381849,3.13381849,3.13381849,3.133818
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4132488,0.04132488,0.04132488,0.04132488,0.04132488,0.04132488,0.041324
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4132488,0.04132488,0.04132488,0.04132488,0.04132488,0.04132488,0.041324
88,0.04132488,0.04132488,0.04132488,0.04132488,0.04132488,0.04132488,0.0
4132488,0.04132488,0.04132488,0.04132488,0.04132488,0.04132488,0.041324
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13,1.10599413,1.10599413,1.10599413,1.10599413,1.10599413,1.10599413,1.1
0599413,1.10599413)),na.action=na.omit)

L[11]=modelCobby2$logLik
K[11]=attributes(logLik(modelCobby2))$df
nm[11]=nrow(dadosg)
aic[11]=-2*L[11]+2*K[11]
aicc[11]=aic[11]+((2*K[11]*(K[11]+1)/nm[11]-K[11]-1))
aicu[11]=aicc[11]+nm[11]*log(nm[11]/(nm[11]-K[11]-1))
caic[11]=-2*L[11]+K[11]*(1+log(nm[11]))
bic[11]=-2*L[11]+K[11]*log(nm[11])
aic3[11]=-2*L[11]+3*K[11]

#########################Wilmink####################

modelWilmink=nlme(PLDC~a+(b*exp(-
0.05*Semana))+C*Semana,fixed=list(a+b+C~1),random=pdDiag(a+b+C~1),contro
l=nlmeControl(minScale=10**-100,maxIter=100000),data=dadosg,start=list(fixed
=c(3.27172482,-1.68965451,-0.04914294)),na.action=na.omit)
intervals(modelWilmink)

modelWilmink=nlme(PLDC~a+(b*exp(-
0.05*Semana))+C*Semana,fixed=list(a~GC-1,b~GC-1,C~GC-
1),random=pdDiag(a+b+C~1),control=nlmeControl(minScale=10**-
100,maxIter=100000),data=dadosg,start=list(fixed=c(3.27172482,3.27172482,3.27
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0.04631158,-0.04631158,-0.0463115)),na.action=na.omit)

L[12]=modelWilmink$logLik
K[12]=attributes(logLik(modelWilmink))$df
nm[12]=nrow(dadosg)
aic[12]=-2*L[12]+2*K[12]
aicc[12]=aic[12]+((2*K[12]*(K[12]+1)/nm[12]-K[12]-1))
aicu[12]=aicc[12]+nm[12]*log(nm[12]/(nm[12]-K[12]-1))
caic[12]=-2*L[12]+K[12]*(1+log(nm[12]))
bic[12]=-2*L[12]+K[12]*log(nm[12])
aic3[12]=-2*L[12]+3*K[12]

##############################Jenkins########################
```

```
 modelJenkins=nlme(PLDC~a*Semana*exp(-
C*Semana),fixed=list(a+C~1),random=pdDiag(a+c~1),control=nlmeControl(minSc
ale=10**-100,maxIter=100000),data=dadosg,start=list(fixed
=c(0.5,0.003)),na.action=na.omit)
modelJenkins=nlme(PLDC~a*Semana*exp(-C*Semana),fixed=list(a~GC-1,C~GC-
1),random=pdDiag(a+C~1),control=nlmeControl(minScale=10**-
100,maxIter=100000),data=dadosg,start=list(fixed=c(0.662179,0.662179,0.662179
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179,0.662179,0.662179,0.662179,0.662179,0.662179,0.662179,0.662179,0.6621
79,0.662179,0.662179,0.662179,0.662179,0.662179,0.662179,0.662179,0.66217
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08067868,0.08067868,0.08067868,0.08067868,0.08067868)),na.action=na.omit)

L[13]=modelJenkins$logLik
K[13]=attributes(logLik(modelJenkins))$df
nm[13]=nrow(dadosg)
aic[13]=-2*L[13]+2*K[13]
aicc[13]=aic[13]+((2*K[13]*(K[13]+1)/nm[13]-K[13]-1))
aicu[13]=aicc[13]+nm[13]*log(nm[13]/(nm[13]-K[13]-1))
caic[13]=-2*L[13]+K[13]*(1+log(nm[13]))
ic[13]=-2*L[13]+K[13]*log(nm[13])
ic3[13]=-2*L[13]+3*K[13]
```

APPENDIX B

PARAMETER CARD FOR GENETIC EVALUATION IN REMLF90

```
DATAFILE
DADOS.txt
TRAITS
6 7 8 9
FIELDS_PASSED TO OUTPUT

WEIGHT(S)

RESIDUAL_VARIANCE
1.0 0.2 0.2 0.2
0.2 1.0 0.2 0.2
0.2 0.2 1.0 0.2
0.2 0.2 0.2 1.0
EFFECT
2 2 2 2 cross alpha
EFFECT
3 3 3 3 cross alpha
EFFECT
4 4 4 4 cross alpha
EFFECT
5 5 5 5 cov
EFFECT
1 1 1 1 cross alpha
RANDOM
animal
FILE
pedi.txt
(CO)VARIANCES
0.8 0.1 0.1 0.1
0.1 0.8 0.1 0.1
0.1 0.1 0.8 0.1
0.1 0.1 0.1 0.8
```