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Genetic analysis of growth curve parameters for beef cattle using Markov Chain Monte Carlo estimation methods

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Abstract

Performances taken into account nowadays in French genetic evaluation of beef cattle consist mainly of young growth characteristics recorded on farm (weight at birth, at 120 and 210 days). Selection for better young growth rate generally implies a correlated increase of mature animal weight. Modelling the entire animal growth will allow the breeders to include selection criteria on different parts of the growth curve and therefore better manage the animal selection. The aim of this study is to use a continuous function of age to model the growth process. For this purpose, a Brody function which has interpretable parameters in terms of growth rate and mature body weight was chosen. The data used in this study came from an experimental Charolais herd, created in 1985-1987 out of 300 pure bred Charolais heifers mated with 60 Charolais bulls. 560 females born in an 11 year period were weighed monthly. Heritabilities and genetic correlations for the Brody parameters were obtained by a Bayesian approach using Gibbs sampling. Heritability for the adult body weight was found to be equal to 0.64 and for the maturing rate 0.31. The genetic correlation between these two parameters was estimated at -0.9 which gives some possibilities to select for animals with high growth rate while keeping a reasonable adult body weight.

Introduction

Beef cattle industry has been taking a great interest in modelling animal growth for many years, in order to provide a mathematical summary of weight evolution with age and use it thereafter to compare or predict animals' performances.

A classical way nowadays to analyse these data is to use longitudinal models such as random regression models (Meyer, 2004) or covariance functions (Arango et al., 2004). However, the main drawback of these models is that they require a quite large number of parameters with no particular biological meaning. On the other hand, previous studies (Kaps et al., 1999) showed the great ability of the parametric Brody function to model growth curves for beef cattle. Moreover, two parameters out of the three constituting this

growth function can be interpreted as mature body weight and maturing rate, which are the two main components of interest to beef cattle breeders.

The aim of this paper is to extend the use of this parametric curve to a genetic analysis by decomposing the three parameters of the curve into a genetic and an environmental component. A similar approach has already been proposed using a Gompertz function for growth curves modelling in rabbit (Blasco et al., 2003) and in chicken (Mignon-Grasteau et al., 2000). This model will be applied to a large beef cattle experimental data set and genetic parameters will be estimated.

Materials and methods

Presentation of the data

Data used in this study came from an experimental Charolais herd (Mialon et al., 2001), created in 1985-1987 out of 300 pure bred Charolais heifers mated with 60 Charolais bulls. In order to have weight measures on a sufficient period of time, only females were considered. The data used in this study consists of 560 females born in an 11 year period (1988-1998) and weighed monthly. At this stage, 9 Age Adjusted Weights at specific ages spread homogeneously between birth and 4,5 years of age (more precisely: 1, 112, 224, 364, 540, 720, 900, 1260, 1620 days) were computed by intrapolation. The dataset also contains 47 missing weights, especially at the lastest ages.

Presentation of the model

After preliminary exploratory analysis and according to several previous studies (Arango et al., 2002), the Brody function was chosen to describe the animal weight evolution with time (Brody, 1945):

$$y_{ij} = a_i(1 - b_i \exp(-k_i\ t_j)) + \epsilon_{ij} \tag{1}$$

where y_{ij} represents the body weight measure for animal i at age j, parameters a_i and k_i can be interpreted as the adult body weight for animal i and its maturing rate, respectively.

The residuals ϵ_{ij} are assumed to be independent, normally distributed with mean zero and variance σ_j^2. According to preliminary analyses, the residual variance was found to be changing with time. To take into account these changes, the evolution of the standard error σ_j is also modelled by a Brody function:

$$\sigma_j = a_\epsilon(1 - b_\epsilon \exp(-k_\epsilon\ t_j)) \tag{2}$$

Each parameter $\boldsymbol{a}$, $\boldsymbol{b}$ and $\boldsymbol{k}$ are decomposed into a genetic and an environmental component using a standard polygenic model. More generally, let $\boldsymbol{p} = (\boldsymbol{a}', \boldsymbol{b}', \boldsymbol{k}')'$. Vector

$\boldsymbol{p}$ can be decomposed as:

$$\boldsymbol{p} = \boldsymbol{X\beta} + \boldsymbol{Zu} + \boldsymbol{e} \tag{3}$$

It is expected in practice that the three coefficients $\boldsymbol{a}$, $\boldsymbol{b}$, and $\boldsymbol{k}$ will be correlated. It is indeed known that the adult body weight and the growth rate are correlated. The genetic effects $\boldsymbol{u}$ are assumed to be normally distributed as: $\boldsymbol{u} \sim \mathcal{N}(0, \boldsymbol{G} \otimes \boldsymbol{A})$, where $\boldsymbol{A}$ is the relationship matrix between individuals, $\boldsymbol{G}$ is of dimension 3×3 and corresponds to the genetic covariance matrix between parameters $\boldsymbol{a}$, $\boldsymbol{b}$, and $\boldsymbol{k}$. The residuals $\boldsymbol{e} = (\boldsymbol{e_a}', \boldsymbol{e_b}', \boldsymbol{e_k}')'$ are also assumed normally distributed as: $\boldsymbol{e} \sim \mathcal{N}(0, \boldsymbol{R} \otimes \boldsymbol{I}_N)$, where $\boldsymbol{R}$ is a 3×3 matrix that corresponds to the environmental covariance matrix between parameters $\boldsymbol{a}$, $\boldsymbol{b}$, and $\boldsymbol{k}$, and $\boldsymbol{I}_N$ is the $(N \times N)$ identity matrix.

Bayesian parameter estimations

This model corresponds to a nonlinear mixed effects model, and classical estimation procedures do not apply. Inference on the parameters has therefore been based on a Gibbs sampling algorithm, as presented by Varona et al. (1997) and Blasco et al. (2003). Priors were chosen to be non-informative for all the parameters. The conditional posterior distributions were normal for parameters $\boldsymbol{a}$, $\boldsymbol{b}$, $\boldsymbol{\beta}$, and $\boldsymbol{u}$, but non standard for parameters $\boldsymbol{k}$ and $\boldsymbol{p_\epsilon} = (a_\epsilon, b_\epsilon, k_\epsilon)'$. A Metropolis-Hastings algorithm was used to sample values from these latter parameter distributions.

Convergence was assessed by overlapping two chains started from different starting values and also by means of the test of Gelman and Rubin (1992). Due to the strong correlations between the different parameters, slow convergence was observed. The Gibbs sampler was run for 300000 iterations with a burn-in period of 100000.

Genetic parameters estimation

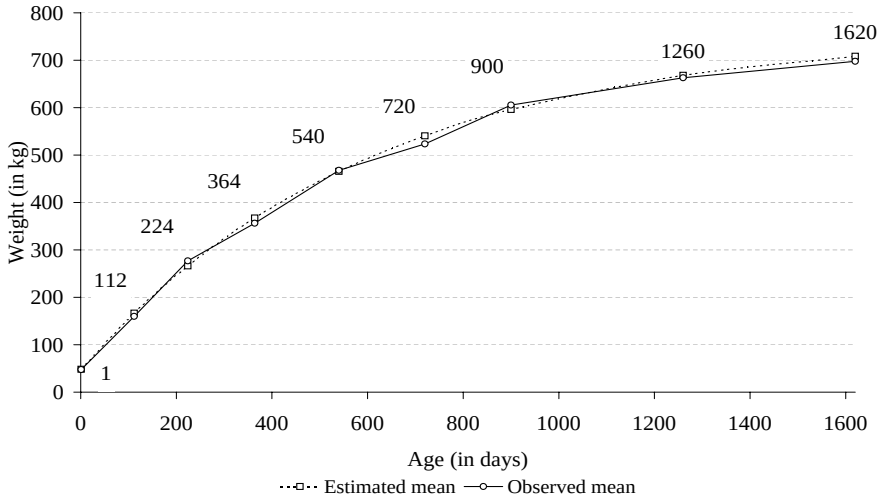
Heritability for each of the Brody curve parameters is computed, using the following definition: $h^2 = \sigma_u^2/(\sigma_u^2 + \sigma_e^2)$, where σ_u^2 is the additive genetic variance and σ_e^2 is the residual variance for parameters $\boldsymbol{a}$, $\boldsymbol{b}$ or $\boldsymbol{k}$. These heritability values are, however, expected to be slightly overestimated as they do not take into account the global residual variances. In order to overcome this drawback a first order Taylor expansion was used and provided corrected heritability estimates for weight at all ages.

Results

Model fitting

The estimated phenotypic values for the average Brody curve were for the three parameters a, b and k: 756, 0.94 and 0.000016, respectively. Figure 1 shows this average Brody curve plotted versus a non-parametric curve, obtained by averaging all weights at each age. The Brody function seems to fit the data very well. The Vonesh concordance coefficient (Vonesh et al., 1996; Jaffrezic et al., 2004) was used to provide a goodness-of-fit value at each age. It has values between -1 and 1 with a perfect fit at 1. This coefficient was found to range between 0.7 and 1, which confirms the adequacy of the Brody function to individual phenotypic curves.

Figure 1: Average phenotypic growth curve



Genetic parameters estimation

Table 1 presents the different parameter estimates: heritability and correlations between the growth curve parameters. Heritability for the adult body weight was found to be quite high, equal to 0.76, whereas heritability for the maturing rate was much lower, equal to 0.31. However, as mentioned in the methodology section, these values are expected to be slightly overestimated. Heritability estimates obtained at the different ages using a first order Taylor expansion are given in Figure 2. The general form of the curve is in

agreement with the results of Koots et al. (1994), with a decrease at early ages followed by an increase when animals get older. Heritability for the mature weight was found equal to 0.64. Several studies have already estimated the heritability of the adult body weight. The heritability values for mature weight range between 0.4 and 0.61 (Kaps et al.,1999). It is, however, more difficult to find references for the calculation of the heritability for the maturing rate, although it is a character of great interest to breeders.

A very interesting feature of the proposed model compared to the classical longitudinal approaches, comes from the fact that it directly provides for each animal in the pedigree a genetic value for the adult body weight as well as for the maturing rate. As shown in Table 1, the genetic correlation between these two traits was found to be equal to -0.9. This will allow the breeders to make an informed selection and to obtain a balance between these two characters. In fact, the aim would be to obtain animals with fast early growth rate without a too dramatic increase of the adult body weight.

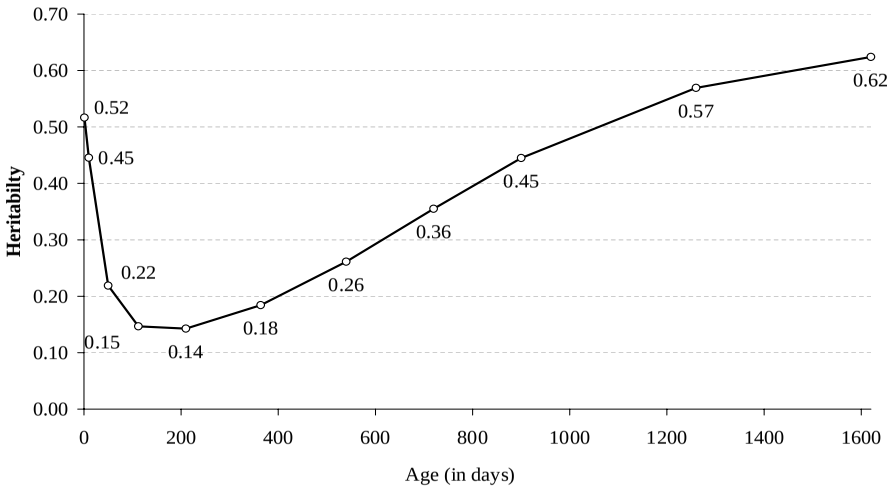
Table 1. Estimates of the heritability and genetic correlations for parameters a, b and k of the Brody curve.

Variable	Mean	Median	Standard Deviation	25% quantile	75% quantile
h^2a	0.76	0.77	0.09	0.70	0.83
h^2b	0.39	0.39	0.09	0.33	0.45
h^2k	0.31	0.31	0.10	0.23	0.38
r_g (ab)	0.42	0.43	0.13	0.34	0.51
r_g (ak)	-0.89	-0.90	0.08	-0.96	-0.85
r_g (bk)	-0.44	-0.45	0.16	-0.56	-0.33

Prediction ability of the model

In order to evaluate the ability of the model to predict adult body weight, the weights at 1620 days were deleted for 50% of the animals (randomly chosen) and predicted using the proposed Brody model, but also with a quartic random regression (RR) and a third order structured antedependence model (SAD) (Jaffrezic et al., 2004). The concordance coefficients between the predicted values and the observed 1620 days weight were equal to 0.64, 0.87, 0.88, for the Brody, RR and SAD models respectively. RR and SAD models therefore seem to be better able to extrapolate the growth curve. Looking at specific animal growth patterns, the parametric Brody growth curve was found, however, to be less influenced by temporary weight variation, such as during the calving time for example,

Figure2: Heritability evolution with age



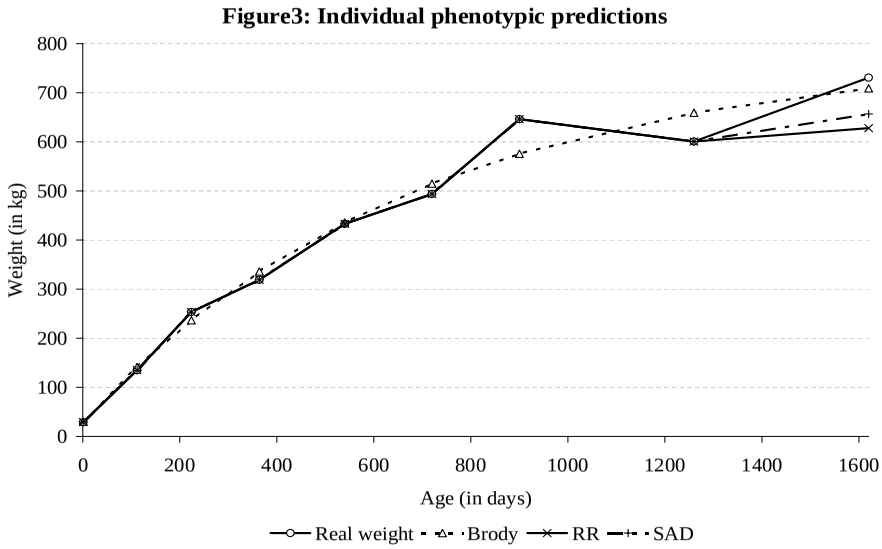
as shown in Figure 3. This approach will therefore give a more general pattern of the animal growth curve.

Discussion

One of the main advantages of the approach presented here is the biological interpretability of the parameters. Two of the Brody curve parameters can in fact be interpreted as the adult body weight and the maturing rate linked to growth rate, respectively, which are the two main components of interest for breeders. The use of this approach in genetic evaluation would therefore lead to two main genetic values for each animal, one for the body weight and one for the maturing rate, which would allow a combined selection on these two components of the growth curve.

Comparison for the prediction ability of the model with other longitudinal approaches such as random regression (Meyer, 2004) and structured antedependence models (Jaffrezic et al., 2004) proved to be in favour of the latter methodologies. By its parametric form the proposed model, however, seems to be less influenced by temporary variation of the weight and therefore gives a more general pattern of the individual growth curve, which could be useful to rank the different animals according to their growth characteristics.

One of the main drawbacks of the proposed approach, however, is the computing time required to estimate the parameters due to the use of MCMC based estimation



procedures. Novel estimation procedures have recently been proposed in the statistical literature for nonlinear mixed effects models, such as the stochastic EM algorithm or the stochastic approximation EM, and it would therefore be worth investigating these different procedures and see if they would be able to substantially reduce the required computing time.

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