Genetic modelling of feed intake in rabbit

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ABSTRACT: Feed intake was recorded weekly for 4,584 rabbits from weaning to 70 days of age (6 weeks). Different character process, orthogonal polynomials and structured antedependence models were fitted to the data in order to model appropriately the structure of the covariance matrices for the genetic, permanent and litter random effects of feed intake. Models were compared using the Bayesian information criterion. The model that best fitted the data and provided good phenotypic covariance matrix estimation was a structured antedependence model of order 2 for the genetic and permanent environmental effects and a uniform correlation matrix with heterogeneous variance for the litter effect. Nonetheless, this model tended to overestimate heritability. Thus, even if it fitted less well to the data, orthogonal polynomial of order 2 that provided a good estimate of the heritability and covariance structures seemed to be the most appropriate model for studying rabbit feed intake.

Keywords: feed intake; covariance matrix; rabbit

Introduction

Improvement of animal sustainability and productivity through nutrition and in particular through precision feeding will become a major issue for animal production. Actually feed cost has always been an important part of the total production cost for all production system (Diaz et al. (2013), Drouilhet et al. (2013), Conintong et al. (2004), Calenge et al. (2014)). Furthermore, improving feed efficiency could reduce animal excretion, and consequently decrease the environmental impact of the production. Thanks to the development of automatic self-feeders and electronic identification (Basso et al. (2014), David et al. (2014), Do et al. (2013)), it is now possible to record feed intake (together with weight for some species) each time an animal access the feeder. Such datasets provide an incredibly rich source of information about the feed intake and growth dynamics of animals. Nonetheless, although a large quantity of literature exists for modelling longitudinal measurements across time (Verbeke and Molendbergh, (1997)), genetic studies on feed efficiency often work on summarized phenotypes or use a simple repeatability model for repeated records (Arthur et al. (2001)) which supposes, too narrowly, a uniform correlation between measurements that can induce bias in the parameter estimations. Other flexible approaches, that consider change in the correlation between measurements with time, exist and have been used to study other traits such as character process (David et al. (2007)), random regression (Huisman et al. (2002)) or structured antedependence models (Jaffrezic et al. (2004)). In order to improve the study of feed consumption and related traits, our objective was to determine the most appropriate model for modelling the covariance structure between successive measurements of feed intake and for estimating genetic parameters. Feed intake data of growing rabbits was used to compare the different models.

Materials and Methods

Rabbit rearing facility and data. Data from rabbits of the paternal line AGP59 of the Hypharm breeding company was used for the analysis. The AGP59 line is selected for weight at 70 days, carcass yield and resistance to digestive disorders. At weaning, four kits of the first litter of each dam were placed in individual pen. They received a commercial pellet ad-libitum until 70 days of age. Feed intake was recorded manually as the difference between weight of feed delivered and refusals for 4,584 rabbits during 6 weeks. A total of 8,813 animals were included in the pedigree.

Statistical analyses. Let \( Y_i(t_j) \) be the feed intake of animal \( i \) during week \( j \). Models used to study feed intake can all be decomposed as follows:

\[
Y_i(t_j) = \mu_i(t_j) + u_i(t_j) + p_i(t_j) + l_k(t_j)
\]

Where \( \mu_i(t_j) \) corresponded to the fixed effects at time \( t_j \) (sex of the young rabbit, litter size at 21 d., year*birth month). \( u_i(t_j) \), \( p_i(t_j) \) and \( l_k(t_j) \) were the genetic, “permanent” (animal effect) and litter random functions independent of one another with covariance functions \( U(t_j, t_{j'}) \), \( P(t_j, t_{j'}) \), \( L(t_j, t_{j'}) \) respectively. The goal of the analysis was to find the most appropriate and parsimonious covariance function for the three random effects. In order to do so, we tested approaches which attempted to model the form of the random effects functions (random regression, structured antedependence models (SAD)) or the covariances functions themselves (character process model (CP), orthogonal polynomials (OP)). The list of models tested for each random effect is presented in Table 1. For a random effect (\( P(t) \) for instance), the general form of the orthogonal polynomials model of order \( k \) is:

\[
P(t) = \sum_{q=0}^{k} p_q \phi_q(t)
\]

\[
P(t_j, t_{j'}) = \sum_{q=0}^{k} \sum_{l=0}^{q} \phi_q(t_j) \phi_l(t_{j'}) \sigma_{p_q p_l}
\]
Where $\phi_q$ is the $q$th Legendre polynomial (Kirkpatrick et al. (1990)). The general form of the structured antedependence model of order $k$ is:

$$p(t_j) = \sum_{s=1}^{k} \theta_{sj} p(t_{j-s}) + e(t_j)$$

where $\theta_{sj}$ is the $s$th antedependence parameter for time $t_j$, $e(t_j)$ is a random normally distributed effect with mean 0 and innovation variance $\sigma^2_p(t_j)$. To reduce the number of parameters in the SAD model, $\theta_{sj}$ and $\sigma^2_p(t_j)$ were assumed continuous functions of time. We chose, for a function of order $n$: $\theta_{sj} = \sum_{q=0}^{n} a_{sq} t_j^q$ and $\sigma^2_p(t_j) = \exp\left(\sum_{q=0}^{n} b_{sq} t_j^q\right)$ (the order can be different for $\theta_{sj}$ and $\sigma^2_p(t_j)$).

Parameters of all models were estimated using restricted maximum likelihood procedures of ASReml (Gilmour et al. (2009)). Comparison among models was based on the Bayesian information criterion (BIC Schwarz (1978)). The best model was the one which maximized the BIC.

Table 1. List of models tested (number of parameters) for each random effect

<table>
<thead>
<tr>
<th>CP1</th>
<th>OP2</th>
<th>SAD3</th>
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<tbody>
<tr>
<td>IDV (1)</td>
<td>OP1 (3)</td>
<td>SAD1-00 (2)</td>
</tr>
<tr>
<td>IDH (7)</td>
<td>OP2 (6)</td>
<td>SAD1-10 (3)</td>
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<tr>
<td>CORUV (2)</td>
<td>SAD1-11 (4)</td>
<td></td>
</tr>
<tr>
<td>CORUH (7)</td>
<td>SAD1-21 (5)</td>
<td></td>
</tr>
<tr>
<td>AR1V (2)</td>
<td>SAD1-22 (6)</td>
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</tr>
<tr>
<td>AR1H (7)</td>
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<td>SAD2-222 (9)</td>
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</tbody>
</table>

Legend: IDV, IDH = diagonal matrix with homogeneous, heterogeneous variance with time, respectively; CORUV, CORUH=uniform correlation with homogeneous, heterogeneous variance with time, respectively; AR1V, AR1H=first order autoregressive correlation with homogeneous, heterogeneous variance with time, US=unstructured covariance matrix.

Results and Discussion

Models comparison. The BIC was chosen to compare non nested models. The score test (Jaffrezic et al. (2003)) has also been proposed to measure the goodness-of-fit of the covariance structure for longitudinal data but is less easy to compute. The model with the highest BIC was a model considering 1) a second order antedependence model for the genetic effect with a quadratic function for the antedependence parameters and the innovation variance, 2) a second order antedependence model for the “permanent” effect with a quadratic function for the first antedependence parameter and a linear function of time for the second antedependence parameter and innovation variance and 3) a uniform correlation matrix with heterogeneous variance with time for the litter effect. The selected SAD model required 33 parameters with a BIC value of -5621 which was much higher than the best OP (quadratic function for $u_i(t_j), p_i(t_j)$ and uniform correlation matrix with heterogeneous variance with time for the litter effect, BIC=-6029.55, 20 parameters), CP model with unstructured covariance structure (US model for $u_i(t_j), p_i(t_j)$, heterogeneous variance for $I_k(t_j)$; BIC=-5725.65, 48 parameters) or simple repeatability model (BIC=-7292, 4 parameters).

Phenotypic correlations and genetic parameters. Phenotypic correlations estimated with a simple repeatability, the best CP, the best OP and the SAD model that best fitted the data are presented in Figure 1. Heritabilities obtained with the same models are presented in Figure 2. The CP model with unstructured covariance structures was the reference model to compare against. The pattern of phenotypic correlations was quite similar for the CP, OP and SAD models. The correlation decreased with the time interval between measurements as is classically reported for longitudinal data. Nonetheless, correlations estimated with the CP model were closer to those of the SAD model than to those of the OP model for short time intervals. In contrast to the phenotypic correlations, heritabilities obtained with the SAD, OP and CP model were quite different. Heritabilities estimated with the CP model showed erratic changes with time with a large increase at 2 weeks of age. SAD model provided heritabilities in the range of that reported in cattle (Arthur et al. (2001)) but much higher than those of the OP model at all time. These estimates also did not show the same pattern with age, since heritability decreased with age in the OP model while the decrease was observed from 3 to 6 weeks of age with the SAD model. Heritabilities of SAD model were also higher than those of the CP model except at 2 and 6 weeks of age. The discrepancy between the different models showed that it seemed difficult to disentangle the genetic from the random animal effect. Thus, we ran the OP, CP and SAD models for the “permanent” effect only and performed the same comparison. Once
again, the model that best fitted the data and provided the best phenotypic covariance matrix in comparison with the CP model with unstructured covariance matrix was the SAD model. Nonetheless, the heritabilities estimated were still higher than those of the CP model. Furthermore, the correlation between EBV was the highest between OP and CP model (>0.99). When comparing OP and SAD models for growth traits, Jaffrezic et al. (2004) also observed that heritabilities of the SAD models were the highest; but they did not have CP model with unstructured covariance matrices estimates to compare with.

Figure 1: Phenotypic correlations estimated with the best OP, CP, simple repeatability models and the model that best fitted the data (SAD)

**Conclusion**

SAD models provided the best fit to the data but overestimated the heritabilities (in comparison with estimates of the CP model with unstructured covariance matrices). Therefore, OP model seemed to be the most suitable approach for studying feed intake in this specific rabbit dataset. Similar analysis should be performed on other traits related to feed efficiency in several species in order to determine, if possible, the most appropriate models for studying these traits.

**Literature Cited**


Calenge, F., Mignon-Grasteau, S., Chanteloup, N. K. et al. (2014). *Avian Pathol.* Published online


