Using group records of feed intake to select for feed efficiency in

rabbit

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Abstract

Models for genetic evaluation of feed efficiency (**FE**) for animals housed in groups when they are either

fed ad libitum (**F**) or on restricted (**R**) feeding were implemented. Definitions of FE on F included group

records of feed intake ($\overline{\mathrm{FI}}_\mathrm{F}$) and individual records of growth rate ($\mathrm{G_F}$) and metabolic weight (**$\mathrm{M_F}$**).

Growth rate (**$\mathrm{G_R}$**) as FE measurement on R was used.

Data corresponded to 5,336 kits from a rabbit sire line, from 1,255 litters in 14 batches and 667 cages.

A five-trait mixed model (also with metabolic weight on R, **$\mathrm{M_R}$**) was implemented including, for each

trait, the systematic effects of batch, body weight at weaning, parity order and litter size; and the

random effects of litter, additive genetic and individual. A Bayesian analysis was performed.

Conditional traits such as $\overline{\mathrm{FI}}_\mathrm{F}|\mathrm{M_F}, \mathrm{G_F}$ and $\mathrm{G_F}|\mathrm{M_F}, \overline{\mathrm{FI}}_\mathrm{F}$ were obtained from elements of additive genetics

($\left(\overline{\mathrm{FI}}_\mathrm{F}|\mathrm{M_F}, \mathrm{G_F}\right)_g$ and $\left(\mathrm{G_F}|\mathrm{M_F}, \overline{\mathrm{FI}}_\mathrm{F}\right)_g$) or phenotypic (($\left(\overline{\mathrm{FI}}_\mathrm{F}|\mathrm{M_F}, \mathrm{G_F}\right)_p$ and $\left(\mathrm{G_F}|\mathrm{M_F}, \overline{\mathrm{FI}}_\mathrm{F}\right)_p$) (co)variance

matrices. In the first case, heritabilities were low (0.07 and 0.06 for $\left(\overline{\mathrm{FI}}_\mathrm{F}|\mathrm{M_F}, \mathrm{G_F}\right)_g$ and $\left(\mathrm{G_F}|\mathrm{M_F}, \overline{\mathrm{FI}}_\mathrm{F}\right)_g$,

respectively) but null genetic correlation between the conditional and conditioning traits is

guaranteed. In the second case, heritabilities were higher (0.22 and 0.16 for $\left(\overline{\mathrm{FI}}_\mathrm{F}|\mathrm{M_F}, \mathrm{G_F}\right)_p$ and

21 $\left(G_F | M_F, \overline{FI}_F \right)_p$, respectively) but the genetic correlation between $\left(\overline{FI}_F | M_F, G_F \right)_p$ and G_F was

22 moderate (0.58). Heritability of G_R was low (0.08). This trait was negatively correlated with

23 $\left(G_F | M_F, \overline{FI}_F \right)_p$ and $\left(G_F | M_F, \overline{FI}_F \right)_g$ of animals on F, which indicate a different genetic background. The

24 correlation between G_R and G_F was also low to moderate (0.48) and the additive variance of G_F was

25 almost 4 times that of G_R, suggesting the presence of a substantial genotype by feeding regimen

26 interaction.

27 **Key words**: feeding regimen, GxE interaction, selection, correlated response, genetic parameters

Introduction

29 Despite economic and environmental importance of improving feed efficiency (**FE**) (Kennedy et al.,

30 1993; Shirali et al., 2012), direct selection for this trait has not been performed in most breeding

31 programs in rabbit mainly because of the problems associated with individual recording of feed intake

32 (**FI**). Indirect selection for average daily gain (**G**) or weight at the end of the growing period has been

33 performed instead (Rochambeau, 1989; Estany et al., 1992; Luckefahr et al., 1996; Piles and Blasco,

34 2003). However, genetic correlation between those traits and FE may not be high enough to result in

35 a significant correlated response (Piles et al. 2004). Therefore, alternative direct selection procedures

36 must be found. Recently, selection for increased G on restricted feeding (**G_R**) has been proposed as

37 selection criteria to improve FE since variation in this trait is directly related to variation in FE because

38 of constant FI (Nguyen et al., 2005). Selection for this trait is expected to yield a greater response on

39 FE than selection for increased average daily gain under full-feeding (**G_F**). Other approaches involve

40 the measurement of individual FI, like selection for residual feed intake (RFI) defined as the difference

41 between actual FI and that predicted from a phenotypic fixed (Koch et al., 1963) or random (Piles et

42 al., 2007; Aggrey and Rekaya, 2013; Sánchez et al., 2017; Shirali et al., 2017) regression of FI on

43 requirements for production and maintenance of body condition. When RFI is calculated at

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44 phenotypic level, there is no phenotypic correlation between residuals (RFI) and the explanatory

45 variables representing animal's needs, but this does not guarantee null genetic correlations. In fact,

46 unfavourable genetic response on growth has been observed after selection for RFI calculated from

47 phenotypic regressions (Gilbert et al., 2007; Cai et al., 2008; Drouilhet et al. 2016). This result was

48 previously shown by Kennedy et al. (1993) who proposed basing the correction of FI not on the

49 phenotypic regression, but on the genetic regression of FI on production traits. They defined

50 "restricted residual feed intake" (**RRFI**), because of its equivalence to a restricted selection index in

51 which production traits are held constant. This definition of RRFI guarantees null genetic correlation

52 with performance traits, and thus null correlated response on them. However, expected direct

53 response would be lower than that of selection based on phenotypic regression (i.e. RFI).

54 Implementation of this definition of FE has been performed using multiple-trait models for individual

55 records of FI (Strathen et al. 2014; Shirali et al., 2018). Only Shirali et al. (2015) used group records of

56 FI to estimate genetic parameters of the classical definition of RFI using a single-trait model with

57 different (but correlated) genetic and permanent effects for each cage mate, which could be

58 considered a different approach. The opportunity of using group records is important because

59 measurement of FI at the group level is feasible and cheaper than individual recording due to the

60 expensive equipment required (Su et al., 2018).

61 In this paper we propose and discuss the use of selection criteria to improve FE of animals housed in

62 groups and fed ad libitum (**F**). Those definitions of FE involve the use of group records of FI and

63 individual records of growth and body weight. In addition, we estimate genetic parameters of G_R and

64 the magnitude of genotype by feeding regimen interaction on FE traits.

Material and Methods

66 **Animals and experimental design**

67 A detailed description of the experiment can be found in Piles et al (2017). In brief, animals came from

68   a rabbit sire line selected for G_F during the fattening period (from 32 to 60 d of age). Animals were

69   bred under constant environmental and management conditions from weaning (32 d) to slaughter

70   age (67 d), except feeding regimen which was F or restricted (**R**). After weaning, kits were randomly

71   assigned to one of these two treatments and were grouped according to two classes of body weight:

72   big size kits (BS, i.e. with a $BW > 700$ g) and small size kits (SS, i.e. with a $BW \leq 700$ g). Animals from

73   the same litter were distributed between both feeding regimens. A maximum of two kits per litter

74   were allocated to the same cage. Actual feed restriction was on average 75 and 74.1% of the *ad libitum*

75   intake in BS and SS kits, respectively. Individual body weight and cage feed intake were systematically

76   recorded weekly during the whole fattening period. All kits were fed the same pellet diet, supplied

77   once per day in a feeder with three places, and water was always available. Feed was changed to a

78   standard food without antibiotics during the last week of fattening. Data from this period were not

79   included in the analysis to avoid the impact that this change could have on the results. In addition,

80   only data from cages containing the initial 8 kits at the end of the fattening were used for the analysis

81   (667 out of 983 cages). Those data corresponded to 5,336 kits from 101 sires and 423 dams in 1,255

82   litters produced in 14 batches (between July 2012 and June 2014) and housed in 667 cages. For the

83   whole control period, individual average daily feed intake in cages on F ($\overline{\textbf{FI}}_{\textbf{F}}$) was computed for each

84   cage as the regression coefficient of cage cumulated mean FI (i.e. cumulated FI/8) on age in days.

85   Likewise, $\textbf{G}_{\textbf{F}}$ and $\textbf{G}_{\textbf{R}}$ were computed for each animal as the regression coefficients of its body weight

86   on age in days for F and R, respectively. In addition, metabolic body weight ($\textbf{M}_{\textbf{F}}$ and $\textbf{M}_{\textbf{R}}$, on F and R,

87   respectively) was computed as the mean of the weekly values computed as the average of individual

88   body weight at the beginning and the end of the corresponding week to the power 0.75.

89   **Statistical Analysis**

90   Variance components for a number of conditional traits reflecting FE were estimated using

91   information from cage records of $\overline{\text{FI}}_{\text{F}}$ and individual records of G_F, M_F, G_R and M_R. A five-trait mixed

92   model was implemented. Model for $\overline{\text{FI}}_{\text{F}}$ can be written as:

93
$$\overline{FI}_{F,ijk} = B_i + S_j + \mathbf{x}'_{POk}\,\mathbf{PO} + \mathbf{x}'_{LSk}\,\mathbf{LS} + \mathbf{z}'_{lk}\,\mathbf{l} + c_k + \mathbf{z}'_{ak}\,\mathbf{a} + \mathbf{z}'_{dk}\,\mathbf{d} + e_{ijk}$$

94   where, $\overline{FI}_{F,ijk}$ is the individual average daily feed intake record of the kth cage on F, in the ith batch and

95   the jth group of size class; $\mathbf{x}'_{POk}, \mathbf{x}'_{LSk}$, $\mathbf{z}'_{lk}$, $\mathbf{z}'_{ak}$ and $\mathbf{z}'_{pk}$are vectors containing the proportion of animals

96   in the kth cage in each level of the factors: parity order, litter size, litter, additive genetic and individual

97   environmental, respectively; the length of those vectors is the number of levels of the corresponding

98   factor. B_i is the effect of the ith batch (14 levels), S_j is the effect of the jth size class (2 levels: BS, SS);

99   **PO** is the vector of parity order effects (4 levels: 1, 2, 3 and >3); **LS** is the vector of litter size effects (7

100   levels: < 6, 6, 7, 8, 9, 10, > 10); **l** is the vector of litter effects (1,255 levels); **a** is the vector of breeding

101   values (6,531 levels, i.e. animals in the pedigree corresponding to 5 generations); **d** is the vector of

102   individual environmental effects (5,336 levels, i.e. animals with records); c_k is the effect of the kth cage

103   (667 levels) and e_{ijk} is the residual.

104   For individually recorded traits (G_F, G_R, M_F and M_R) exactly the same model was used, but now the

105   design vectors $\mathbf{x}'_{POk}, \mathbf{x}'_{LSk}$, $\mathbf{z}'_{lk}$, $\mathbf{z}'_{ak}$ and $\mathbf{z}'_{dk}$ contained either 0 or 1.

106   In a Bayesian framework, this model corresponds to the expectation of the distribution of the data

107   given model parameters –conditional likelihood; in our case, a multivariate normal distribution was

108   considered. The systematic effects, **B** and **S**, were assumed *a priori* to follow uniform distributions.

109   The *a priori* distribution of the additive genetic effect was $p(\mathbf{a}|\mathbf{G})\sim N(\mathbf{0}, \mathbf{G} \otimes \mathbf{A})$, where **G** is the 5 × 5

110   additive genetic covariance matrix between traits and **A** is the numerator relationship matrix, of

111   dimension N, equal to the number of individuals in the pedigree. The *a priori* distribution of litter

112   effects, cage environmental effects and individual environmental effects were $p(\mathbf{l}|\mathbf{L})\sim N(\mathbf{0}, \mathbf{L} \otimes \mathbf{I_l})$,

113    $p(\mathbf{c}|\mathbf{C})\sim N(\mathbf{0}, \mathbf{C} \otimes \mathbf{I_c})$ and $p(\mathbf{d}|\mathbf{D})\sim N(\mathbf{0}, \mathbf{D} \otimes \mathbf{I_d})$, respectively, where **l**, **c** and **d** are the

114   corresponding vectors of environmental effects, **L, C** and **D** are the corresponding 5 × 5 covariance

115   matrices, and $\mathbf{I_l}$, $\mathbf{I_c}$ and $\mathbf{I_d}$ are unit matrices of dimension equal to the number of levels of each factor

116   (i.e. 1,303, 667 and 5,336, respectively). Similarly, the distribution of the residual effects was

117 $p(\mathbf{e}|\mathbf{R}) \sim N(\mathbf{0}, \mathbf{R} \otimes \mathbf{I_e})$, where $\mathbf{R}$ is the corresponding residual covariance matrix between traits and $\mathbf{I_e}$

118 is the identity matrix.

119 Explicitly, the aforementioned covariance matrices were the following symmetric matrices:

120 $$\mathbf{G} = \begin{bmatrix} \sigma^2_{g;FI_F} & \sigma_{g;FI_F,G_F} & \sigma_{g;FI_F,M_F} & \sigma_{g;FI_F,G_R} & \sigma_{g;FI_F,M_R} \\ & \sigma^2_{g;G_F} & \sigma_{g;G_F,M_F} & \sigma_{g;G_F,G_R} & \sigma_{g;G_F,M_R} \\ & & \sigma^2_{g;M_F} & \sigma_{g;M_F,G_R} & \sigma_{g;M_F,M_R} \\ & & & \sigma^2_{g;G_R} & \sigma_{g;G_R,M_R} \\ & & & & \sigma^2_{g;M_R} \end{bmatrix},$$

121 $$\mathbf{L} = \begin{bmatrix} \sigma^2_{l;FI_F} & \sigma_{l;FI_F,G_F} & \sigma_{l;FI_F,M_F} & \sigma_{l;FI_F,G_R} & \sigma_{l;FI_F,M_R} \\ & \sigma^2_{l;G_F} & \sigma_{l;G_F,M_F} & \sigma_{l;G_F,G_R} & \sigma_{l;G_F,M_R} \\ & & \sigma^2_{l;M_F} & \sigma_{l;M_F,G_R} & \sigma_{l;M_F,M_R} \\ & & & \sigma^2_{l;G_R} & \sigma_{l;G_R,M_R} \\ & & & & \sigma^2_{l;M_R} \end{bmatrix},$$

122 $$\mathbf{C} = \begin{bmatrix} \sigma^2_{c;FI_F} & \sigma_{c;FI_F,G_F} & \sigma_{c;FI_F,M_F} & 0 & 0 \\ & \sigma^2_{c;G_F} & \sigma_{c;G_F,M_F} & 0 & 0 \\ & & \sigma^2_{c;M_F} & 0 & 0 \\ & & & \sigma^2_{c;G_R} & \sigma_{c;G_R,M_R} \\ & & & & \sigma^2_{c;M_R} \end{bmatrix},$$

123 $$\mathbf{D} = \begin{bmatrix} \sigma^2_{d;FI_F} & \sigma_{d;FI_F,G_F} & \sigma_{d;FI_F,M_F} & 0 & 0 \\ & \sigma^2_{d;G_F} & \sigma_{d;G_F,M_F} & 0 & 0 \\ & & \sigma^2_{d;M_F} & 0 & 0 \\ & & & \sigma^2_{d;G_R} & \sigma_{d;G_R,M_R} \\ & & & & \sigma^2_{d;M_R} \end{bmatrix} \text{ and}$$

124 $$\mathbf{R} = \begin{bmatrix} \sigma^2_{e;FI_F} & 0 & 0 & 0 & 0 \\ & \sigma^2_{e;G_F} & \sigma_{e;G_F,M_F} & 0 & 0 \\ & & \sigma^2_{e;M_F} & 0 & 0 \\ & & & \sigma^2_{e;G_R} & \sigma_{e;G_R,M_R} \\ & & & & \sigma^2_{e;M_R} \end{bmatrix}$$

125 Bounded uniform priors were assumed for the elements of **G**, **L**, **C**, **D** and **R**.

126   Cage effects on $\overline{\mathrm{FI}}_\mathrm{F}$ and environmental individual effects on individually recorded traits are necessary

127   factors to take into account properly the environmental covariance between $\overline{\mathrm{FI}}_\mathrm{F}$ and individually

128   recorded traits. If these effects were not considered, part of this environmental covariance could be

129   assigned to genetic covariance. Thus, although these effects would not be identifiable in univariate

130   models they are necessary in a multivariate setting. In this multivariate scenario, covariance between

131   traits allows for the identification of cage effects on $\overline{\mathrm{FI}}_\mathrm{F}$ and environmental individual effects on

132   individually recorded traits ($\mathrm{G_F}$, $\mathrm{G_R}$, $\mathrm{M_F}$ and $\mathrm{M_R}$), but given that the amount of information to separate

133   them from the residual effects is limited, total environmental variance was defined as the addition of

134   cage, individual environmental and residual variance components ($\mathbf{E} = \mathbf{C} + \mathbf{D} + \mathbf{R}$) in each sampling

135   iteration. Samples of elements of $\mathbf{R}$ matrix related to $\overline{\mathrm{FI}}_\mathrm{F}$ were previously multiplied by 8 (i.e. the

136   number of animals in a cage) to rescale them to variation at individual level, instead of mean level.

137   Finally, total phenotypic variance matrix was defined as $\mathbf{P} = \mathbf{G} + \mathbf{L} + \mathbf{E}$

138   Phenotypic and genetic RFI definitions are equivalent to selection indexes based on the component

139   traits with weights equal to the corresponding partial regression coefficients at a negative value

140   (Kennedy et al, 1993). Phenotypic and genetic variance-covariance matrices for those selection

141   indexes were defined as was shown by Kennedy et al. (1993) and recently implemented by Shirali et

142   al. (2018): $\boldsymbol{I_G} = \boldsymbol{b'Gb}$ and $\boldsymbol{I_P} = \boldsymbol{b'Pb}$. In our case, $\boldsymbol{b}$ matrix is composed of 5 columns, one for each

143   original trait, and 9 rows. The first five rows correspond to indexes only involving the original traits.

144   The following two rows correspond to indexes which are equivalent to conditional traits with respect

145   to the phenotypic variance-covariance matrix, and the last two rows correspond to indexes which are

146   equivalent to conditional traits with respect to the genetic variance-covariance matrix. These two sets

147   of either phenotypic or genotypic conditional traits correspond to feed intake conditional on growth

148   and metabolic weight under full feeding ($\overline{\mathrm{FI}}_\mathrm{F}|\mathrm{G_F}, \mathrm{M_F}$) (i.e. residual feed intake, Kennedy et al., 1993)

149   and growth conditional on feed intake and metabolic weight, all of them on full feeding ($\mathrm{G_F}|\overline{\mathrm{FI}}_\mathrm{F}, \mathrm{M_F}$)

150   (i.e. residual growth, Crowley et al., 2010). As indicated by Kennedy et al. (1993), conditioning with

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151   respect to the distribution of genetic effects $\left(\left(\overline{FI}_F|G_F, M_F\right)_g\right.$ and $\left.\left(G_F|\overline{FI}_F, M_F\right)_g\right)$ would guarantee a

152   null genetic correlation between conditioned and conditioning traits. When the conditional is effected

153   with respect to the phenotypic distribution of the recorded traits $\left(\left(\overline{FI}_F|G_F, M_F\right)_p\right.$ and $\left.\left(G_F|\overline{FI}_F, M_F\right)_p\right)$,

154   the phenotypic correlation between those traits is null but the genetic correlation is not guaranteed

155   to be so.

156   In order to illustrate the computation of each row of the **b** matrix, we present the cases for

157     $\left(\overline{FI}_F|G_F, M_F\right)_g$ and $\left(\overline{FI}_F|G_F, M_F\right)_p$, assuming that the order of the traits in the covariance matrix is $\overline{FI}_F$,

158   G_F, G_R, M_F and M_R.

159   For the case in which the conditional is effected with respect to the additive genetic effects

160   distribution of the recorded traits, the b matrix is:

161     $\boldsymbol{b}_{(FI_F|G_F, M_F)_g} = \begin{bmatrix} 1 & -b_{g;FI_F|G_F} & 0 & -b_{g;FI_F|M_F} & 0 \end{bmatrix}$,

162   Where $b_{g;FI_F|G_F}$ and $b_{g;FI_F|M_F}$ are computed as

$$\begin{bmatrix} b_{g;FI_F|G_F} \\ b_{g;FI_F|M_F} \end{bmatrix} = \begin{bmatrix} \sigma_{g;FI_F,G_F} & \sigma_{g;FI_F,M_F} \end{bmatrix} \begin{bmatrix} \sigma_{g;G_F}^2 & \sigma_{g;G_F,M_F} \\ \sigma_{g;G_F,M_F} & \sigma_{g;M_F}^2 \end{bmatrix}^{-1};$$

164   When the conditional is effected with respect to the phenotypic distribution of the recorded traits,

165   the b matrix is:

166     $\boldsymbol{b}_{(FI_F|G_F, M_F)_p} = \begin{bmatrix} 1 & -b_{p;FI_F|G_F} & 0 & -b_{p;FI_F|M_F} & 0 \end{bmatrix}$,

167   Where $b_{p;FI_F|G_F}$ and $b_{p;FI_F|M_F}$ were computed as

168
$$\begin{bmatrix} b_{p;FI_F|G_F} \\ b_{p;FI_F|M_F} \end{bmatrix} = \begin{bmatrix} \sigma_{p;FI_F,G_F} & \sigma_{p;FI_F,M_F} \end{bmatrix} \begin{bmatrix} \sigma^2_{p;G_F} & \sigma_{p;G_F,M_F} \\ \sigma_{p;G_F,M_F} & \sigma^2_{p;M_F} \end{bmatrix}^{-1}.$$

169 The adopted Bayesian MCMC framework is the optimal to characterize the posterior distributions of

170 the variance-covariance matrix involving the described conditional traits, i.e. selection indexes. Single

171 chains of 1,000,000 iterations were run discarding the first 200,000. Samples of the parameters of

172 interest were saved every 100 rounds. Samples from the marginal posterior distributions of the

173 variance components of the defined selection indexes, at genetic ($I_G = b'Gb$) and at phenotypic

174 ($I_P = b'Pb$) levels, were obtained in each round of the Gibbs sampler.

Results

176 Table 1 shows summary statistics of the analysed traits. As expected, growth mean was larger for

177 animals on F than R because of the limited amount of food provided to animals on R. However,

178 variation was slightly higher for G_R than for G_F (the coefficients of variation were 0.17 and 0.21 on F

179 and R, respectively).

180 All variance components were higher for animals on F than for animals on R, particularly the

181 phenotypic variance for G, which was 1.5 times larger for animals on F than for animals on R (63.34 vs

182 44.08) . The heritability was nearly three times larger for G_F than for G_R (posterior mean 0.21 vs 0.08),

183 but the ratio of phenotypic variance due to litter effects was higher on R than F (Table 2). With regard

184 to the environmental variance –the sum of cage, individual environment, and residual variances -

185 relative to the phenotypic variance, a larger effect was observed for G_R than for G_F (posterior mean

186 [posterior s.d.]: 0.75 [0.03] vs 0.67 [0.04]). The differences between M_R and M_F for variance

187 components were much smaller than those observed between G_R and G_F. Thus, in both metabolic

188 weight traits heritability was around 0.35, being the ratio of litter effect variance to phenotypic

189 variance around 0.25. Cage average feed intake showed a heritability of 0.32. For this trait, litter

190 effects played a much smaller role, the ratio of litter effect variance relative to phenotypic variance

191 being just 0.07.

192 Differences in genetic variances and genetic correlation lower than 1 indicates the existence of

193 genotype by feeding regimen interaction. For G, the genetic correlation (Table 3 and Figure 1) was just

194 0.49 [0.15] while for M this correlation was 0.87 [0.04], clearly showing that the magnitude of the

195 interaction between the genotype and feeding regimen is much larger for growth rate than for

196 metabolic weight. Within each feeding regimen, the genetic correlations between G and M were

197 moderate to high, being the estimates 0.63 [0.09] on F and 0.78 [0.08] on R. The genetic correlations

198 of $\overline{FI}_F$ with G_F and M_F were moderate to high (0.87 [0.06] and 0.60 [0.12], respectively) whereas it was

199 moderate (0.70 [0.9]) with G_R and low (0.24 [0.15]) with M_R.

200 The pattern of litter effect correlations (Table 3) was slightly different to that observed for the genetic

201 correlations. For example, the posterior mean [posterior s.d.] of litter effect correlation between

202 growth across the two feeding regimens was 0.73 [0.11], indicating that the interaction between litter

203 effects and feeding regimen was smaller than the interaction between the genotype and feeding

204 regimen. Within each feeding regimen, the litter effect correlations between growth and metabolic

205 weight were 0.35 [0.09] and 0.47 [0.07] on F and R, respectively. Litter effect correlations of $\overline{FI}_F$ with

206 other traits were null for growth on both feeding regimens and high (above 0.8) with metabolic body

207 weight on both feeding regimens also

208 The environmental correlation could only be estimated for the traits recorded on the same feeding

209 regimen, because there were no individual records taken on the two alternative feeding regimens.

210 The environmental correlation between G_F and M_F and between G_R and M_R were both moderate to

211 high (0.79 [0.03] and 0.75 [0.02], respectively). The environmental correlation of $\overline{FI}_F$ with G_F and M_F

212 were moderate, (0.47 [0.11] and 0.45 [0.10], respectively).

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213   Table 4 shows mean and standard deviation of marginal posterior distributions of variance

214   components and ratios of phenotypic variance for different conditional traits. When the conditional

215   is based on the distribution of the additive genetic effects, the heritability is lower than the

216   corresponding to the conditional on the phenotypic distribution of the recorded traits. The estimated

217   value for $\left(\overline{FI}_F \mid M_F, G_F\right)_p$ was 0.22 [0.08] while that for $\left(\overline{FI}_F \mid M_F, G_F\right)_g$ was only 0.07 [0.04].

218   Similarly, for RG traits the heritability estimates were 0.16 [0.04] and 0.06 [0.03] for

219    $\left(G_F \mid M_F, \overline{FI}_F\right)_p$ and $\left(G_F \mid M_F, \overline{FI}_F\right)_g$, respectively.

220   As expected, the estimated genetic correlations between conditional traits effected on the

221   distribution of additive genetic effects, and the conditioning traits is null (Figure 1). When the

222   conditional is based on the phenotypic distribution of the traits, these genetic correlations between

223    $\left(\overline{FI}_F \mid M_F, G_F\right)_p$ and G_F and M_F were 0.58 and 0.10, respectively, and 0.26 and -0.35 between

224    $\left(G_F \mid M_F, \overline{FI}_F\right)_p$ and $\overline{FI}_F$ and M_F, respectively. The genetic correlations between residual growth

225   and RFI traits are very different depending on whether genetic or phenotypic distributions were used

226   for conditioning. In the first case, a high and negative genetic correlation (-0.8) was obtained while in

227   the second case, the correlation was moderate and positive (0.42, Figure 1). Within type-of-efficiency

228   trait, i.e. residual growth or RFI, the genetic correlation between definitions based on genetic or

229   phenotypic conditioning was, in both cases, 0.68. The estimated genetic correlations between

230   conditional feed efficiency traits and G_R followed the same pattern regardless of conditioning based

231   on phenotypic or genetic relationships between traits. It was low to moderate and positive with RFI

232   traits (0.39 with $\left(\overline{FI}_F \mid M_F, G_F\right)_p$ and 0.48 with $\left(\overline{FI}_F \mid M_F, G_F\right)_g$), and low to moderate but

233   negative with residual growth traits (-0.47 with $\left(G_F \mid M_F, \overline{FI}_F\right)_p$ and -0.43 with $\left(G_F \mid M_F, \overline{FI}_F\right)_g$)

234   **Discussion**

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235   In this study we have reported variance components and genetic parameters of several measurements

236   of feed efficiency obtained from a model that combines group/cage records of FI and individual

237   records of G and M, under two different feeding regimens commonly applied in rabbit meat

238   production farms. This procedure overcomes difficulties for identification of genetic and

239   environmental random effects of FI when group records are used, as was discussed by Su et al. (2018).

240   In addition, it takes advantage of the definition of FE traits as selection indexes that can be obtained

241   from multiple-trait genetic evaluations (Kennedy et al, 1993). The proposed model includes several

242   random factors of variation such as additive genetic, litter, cage and individual environmental effects.

243   They can be identified due to the genetic and environmental correlation between cage FI and

244   individually recorded production traits. Kennedy et al. (1993) showed that selection based on the

245   traditional RFI definition would yield direct response on efficiency at the expense of a reduction in

246   growth and production traits. To overcome this issue, they defined RRFI as RFI based on genotypic

247   regression rather than on phenotypic regression. Selecting for RRFI, direct response would be lower

248   than that achieved by selection on RFI but no unwanted correlated response on growth would be

249   expected. In our study, we clearly confirm these theoretical results. Thus, for our population, we can

250   predict that selection for $\left(G_F \mid M_F, \overline{FI}_F\right)_g$ or $\left(\overline{FI}_F \mid M_F, G_F\right)_g$ would hardly produce any response in

251   FE of the animals. On the contrary, the selection for increasing $\left(G_F \mid M_F, \overline{FI}_F\right)_p$ or reducing

252    $\left(\overline{FI}_F \mid M_F, G_F\right)_p$ will improve FE, but at the expense of an increase in FI and a reduction in G,

253   respectively. As noted by Kennedy et al (1993) heritability is generally higher for RFI than for RRFI

254   because heritability of RRFI is the proportion of the variance of FI which is genetically independent of

255   production. From an applied perspective, the increase in FI could be achieved more easily than the

256   reduction in G. Thus, based on our results, it could be recommended to focus on residual growth

257   rather than on RFI. Another alternative could be to use breeding value predictions for $\left(G_F \mid M_F, \overline{FI}_F\right)_p$

258   or $\left(\overline{FI}_F \mid M_F, G_F\right)_p$ and for G_F and $\overline{FI}_F$ to define a selection index for the efficiency traits with

259   restriction on G_F and $\overline{FI}_F$. Nevertheless, this procedure would yield similar results, in terms of

260   responses in FE, to those expected when $\left(G_F \mid M_F, \overline{FI}_F\right)_g$ or $\left(\overline{FI}_F \mid M_F, G_F\right)_g$ are used as selection

261   criteria. In spite of the limited interest of $\left(G_F \mid M_F, \overline{FI}_F\right)_g$ or $\left(\overline{FI}_F \mid M_F, G_F\right)_g$ as selection criteria, it is

262   relevant to observe that the genetic correlation between them is negative and strong (-0.8). This

263   indicates different biological processes involved in both FE definitions. $\overline{FI}_F \mid M_F, G_F$ would be related to

264   processes involving the limitation of energy and nutrient resource wastage, whereas $G_F \mid M_F, \overline{FI}_F$ would

265   be related to metabolic pathways involved in the efficacy of using those acquired resources for

266   growth. On the contrary, the genetic correlation between $\left(G_F \mid M_F, \overline{FI}_F\right)_p$ and $\left(\overline{FI}_F \mid M_F, G_F\right)_p$ is

267   positive, which is a consequence of $\left(\overline{FI}_F \mid M_F, G_F\right)_p$ not being genetically independent from $\mathbf{G_F}$.

268   Direct selection for FE is difficult and expensive to implement because it requires feed intake

269   recording. The ideal situation would be to record FI at individual level, even when the animals are

270   raised in groups. This can be achieved in species, like pigs and cattle, for which automatic recording

271   feeding systems are available. However, this is not yet the case in rabbit production, so direct selection

272   for FE has been conducted until now by recording feed intake in a small proportion of selection

273   candidates raised in individual cages (Drouilhet et al., 2016). This strategy could limit the progress of

274   genetic selection for FE because of the low accuracy of genetic evaluation of FE for most selection

275   candidates, many of which do not have their own records. In this selected population, heritability of

276   RFI has been reported to be 0.16 (Drouilhet et al., 2013). To our knowledge, no estimates of heritability

277   for RG in rabbit have been reported in the literature.

278   Even in the situation in which electronic feeders are available, it is interesting to explore other sources

279   of information which are less expensive than FI records obtained with them, as it could be FI recorded

280   at the group level (Su et al., 2018). Several studies have reported models for the estimation of genetic

281   parameters and variance components of FI using group data (Olson et al., 2006; Biscarini et al. 2008;

282   Cooper et al., 2010; Su et al., 2018; Shirali et al., 2018) but only Shirali et al. (2015) combine individual

283   records of production traits and group records of FI in a single-trait model defining phenotypic RFI

284   from a phenotypic regression model of cage FI on body weight of each of the two cage mates. This

285   situation is similar to ours but in our case, given that groups are larger (8 cage mates), the number of

286   available cage records is limited (321). Thus, these records by themselves include a limited amount of

287   information and the consideration of information from correlated traits recorded individually, growth

288   and metabolic weights, is mandatory in order to obtain reliable estimations and predictions from the

289   cage-record model. Therefore, our procedure allows us to obtain predictions of breeding values for

290   phenotypic and genetic definitions of RFI proposed by Kennedy et al. (1993) from a multiple-trait

291   model combining individual and cage records., which has never been performed before

292   **Feed efficiency measurements when animals are raised under restricted feeding**

293   Selection for G_R has been proposed as a strategy to select for FE (Nguyen & McPhee 2005, Nguyen et

294   al., 2005). When animals are raised individually and under feed restriction, so that the same amount

295   of feed is provided to all the animals, their growth represents a direct measurement of FE. In those

296   conditions, variation in growth is directly related to variation in FE because of constant FI (Nguyen et

297   al., 2005) and therefore, individual records of FI are not required. This is partially equivalent to the

298   definition of $G_F | M_F, \overline{FI}_F$ if the role of M_F is ignored. When the animals are raised in collective cages,

299   which is our case, within-cage variation in FI might exist, and the meaning of G_R as a FE trait is not

300   clear. The magnitude of the genetic correlations with FE traits defined for animals raised on F could

301   aid to our understanding of the value of G_R as a FE trait.

302   Genetic variance and heritability (0.08) of G_R for animals raised in groups were both low. Therefore, it

303   would be difficult to achieve a positive response to selection for this trait when the animals are raised

304   in collective cages. In addition, G_R seems to be only moderately correlated to any FE trait on F and the

305   sign of those correlations is the opposite to the ones expected between the different measures of FE

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306   assessed, being positive between G_R and $\overline{FI}_F|M_F, G_F$ and negative between G_R and $G_F|M_F, \overline{FI}_F$ (Figure

307   1). The reason to expect opposite signs in the estimated correlations is related to the observed

308   antagonism between $\overline{FI}_F|M_F, G_F$ and $G_F|M_F, \overline{FI}_F$. These results hold regardless of the efficiency trait

309   defined by conditioning on the phenotypic or on the genetic covariance matrix. Therefore, based on

310   these results it seems that G_R of animals in groups seems not to be linked to any biological process

311   involved in FE, at least to those definitions of FE on F. Piles et al (2017) have shown that social genetic

312   effects contribute substantially to total genetic merit of rabbits raised on R when collective cages are

313   used. Models accounting for these indirect genetic effects have shown that the correlation between

314   these effects and direct genetics effects is negative when animals are fed on R. Thus, the existence of

315   this negative correlation could explain the observed correlation between G_R and feed efficiency

316   definitions on F. This unfavourable genetic correlation between direct and indirect genetic effects

317   greatly compromise the success, in terms of response to selection, of any selection process

318   considering G_R on animals raised in collective cages.

319   **Genotype by feeding regimen interaction**

320   Feed restriction during the first two or three weeks of the growth period has become a common

321   practice in commercial farms because of its positive effect on animal health in the presence of diseases

322   that cause digestive disorders (Gidenne et al., 2012). With this practice, farmers also take advantage

323   of an improved efficiency in the use of feed, mainly as a consequence of the compensatory growth

324   that is observed at the end of the growing period when rabbits are fed on F. If the animals in the

325   nucleus are selected on F but are raised on R in rabbit commercial farms, genetic gain achieved in a

326   breeding program for improving FE could not be transferred to production farms due to the effect of

327   a potential interaction between the genotype and the feeding regimen on this trait. We have

328   estimated variance components and genetic parameters of different measures of FE for animals fed

329   on different feeding regimens. Our results support the idea that G_R and G_F or FE on F are traits with

330   different genetic backgrounds, since the genetic correlation between them is not high (0.48 between

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331   G_R and G_F, Table 3 and Figure 1; $0.38 - 0.48$ between G_R and $\overline{FI}_F|M_F, G_F$ Figure 1; and $-0.47 - -0.43$

332   between G_R and $G_F|M_F, \overline{\overline{FI}}_F$ Figure 1). On the other hand, additive genetic variance of G_F is almost 4

333   times the genetic variance of G_R. The different genetic variances and a genetic correlation lower than

334   1 clearly indicate the existence of genotype by feeding regimen interaction (Kolmodin 2003).

335   Therefore, if commercial farms produce young rabbits on R, it would be necessary to evaluate which

336   selection procedure yields the highest response in the production farms: selection for G_R, taking into

337   account indirect effects despite its low variability and heritability, or selection on G_F clearly subject to

338   a strong genotype by feeding regimen interaction, but having a large variability and heritability.

339   In conclusion, group records of FI and individual records of production traits can be jointly used for

340   selection to improve FE. Measurements of FE on R and F in animals raised in groups are correlated at

341   a low level indicating that the magnitude of the genotype by feeding regimen interaction is important,

342   probably as a consequence of the existence of substantial indirect genetic effects especially when

343   animals are on R. In addition, selection for increased G_R could be ineffective at improving FE because

344   of its low heritability on those housing conditions.

Declarations

345

346   **Ethics approval and consent to participate**

347   The research protocol was approved by the animal care and use committee of the Institut de Recerca

348   i Tecnologia Agroalimentàries (IRTA).

349   **Availability of data and material**

350   The datasets used and analysed during the current study are available from the corresponding author

351   on reasonable request.

352   **Competing interests**

353   The authors declare that they have no competing interests

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Table 1. Summary statistics

Trait	Abbreviation	N	Mean	sd
Cage Mean Average Daily Feed Intake on Ad libitum feeding	$\overline{FI}_F$	321	166.2	21.2
Average Daily Gain on Ad libitum feeding	G_F	2568	48.2	8.0
Metabolic Body Weight on Ad libitum feeding	M_F	2568	242.6	25.8
Average Daily Gain on Restricted Feeding	G_R	2768	38.7	8.2
Metabolic Body Weight on Ad libitum feeding	M_R	2768	220.2	25.9

Table 2. Posterior mean (posterior s.d.) of variance components and ratios of phenotypic variance of recorded traits

Factor/parameter	$\overline{FI}_F$[a]	G_F[a]	G_R[a]	M_F[a]	M_R[a]
Litter	50.67 (5.93)	7.52 (1.4)	7.63 (1.12)	87.89 (10.24)	78.87 (8.29)
Additive	247.58 (66.23)	13.35 (3.11)	3.47 (0.85)	138.96 (24.3)	98.21 (16.63)
Environmental	479.83 (117.23)	42.47 (2.37)	32.98 (1.24)	136.34 (13.68)	123.24 (9.9)
Phenotypic	778.08 (117.54)	63.34 (2.13)	44.08 (1.31)	363.19 (13.61)	300.32 (10.58)
$h^{2,b}$	0.32 (0.09)	0.21 (0.05)	0.08 (0.02)	0.38 (0.06)	0.33 (0.05)
$l^{2,b}$	0.07 (0.01)	0.12 (0.02)	0.17 (0.02)	0.24 (0.03)	0.26 (0.03)

[a] $\overline{FI}_F$: cage mean of average daily feed intake on ad libitum feeding; G_F average daily growth on ad libitum feeding; M_F: metabolic body weight on ad libitum feeding; G_R average daily growth on restricted feeding; M_R: metabolic body weight on restricted feeding
[b] h^2: heritability; l^2: litter variance relative to phenotypic variance

Table 3. Posterior mean (posterior s.d.) of correlations due to different factors

	$\overline{FI}_F - G_F$	$\overline{FI}_F - G_R$	$\overline{FI}_F - M_F$	$\overline{FI}_F - M_R$	$G_F - G_R$	$G_F - M_F$	$G_F - M_R$	$G_R - M_F$	$G_R - M_R$	$M_F - M_R$
rhoC	-0.18 (0.1)	-0.05 (0.1)	0.84 (0.04)*	0.81 (0.05)*	0.73 (0.11)*	0.35 (0.09)*	0.33 (0.1)*	0.25 (0.1)*	0.47 (0.07)*	0.92 (0.03)*
rhoG	0.87 (0.06)*	0.71 (0.09)*	0.6 (0.12)*	0.24 (0.15)	0.49 (0.15)*	0.63 (0.09)*	0.19 (0.15)	0.85 (0.07)*	0.78 (0.08)*	0.87 (0.04)*
rhoE	0.47 (0.11)*	--	0.45 (0.1)*	--	--	0.79 (0.03)*	--	--	0.75 (0.02)*	--
rhoP	0.51 (0.07)*	0.11 (0.03)*	0.53 (0.05)*	0.18 (0.05)*	0.17 (0.03)*	0.64 (0.02)*	0.11 (0.04)*	0.2 (0.03)*	0.64 (0.01)*	0.54 (0.04)*

[a] $\overline{FI}_F$: cage mean of average daily feed intake on ad libitum feeding; G_F average daily growth on ad libitum feeding; M_F: metabolic body weight on ad libitum feeding; G_R average daily growth on restricted feeding; M_R: metabolic body weight on restricted feeding

[b] rhoC: correlation due to litter effects; rhoG: genetic correlation; rhoE: environmental correlation; rhoP: phenotypic correlation

Table 4. Posterior mean (posterior s.d.) of variance components and ratios of phenotypic variance of conditional traits

Factor/parameter	$\left(\overline{FI}_F \mid M_F, G_F\right)_p{}^a$	$\left(G_F \mid M_F, \overline{FI}_F\right)_p{}^a$	$\left(\overline{FI}_F \mid M_F, G_F\right)_g{}^a$	$\left(G_F \mid M_F, \overline{FI}_F\right)_g{}^a$
Litter	42.08(14.66)	9.95(1.25)	177.06(63.93)	11.09(1.99)
Additive	111.15(40.07)	5.49(1.41)	52.98(26.09)	2.64(1.14)
Environmental	354.66(74.41)	19.31(1.75)	585.65(148.23)	31.82(8.05)
Phenotypic	507.89(73.22)	34.76(2.06)	815.69(188.8)	45.55(8.19)
$h^{2,b}$	0.22(0.08)	0.16(0.04)	0.07(0.04)	0.06(0.03)
$l^{2,b}$	0.08(0.03)	0.29(0.04)	0.21(0.05)	0.25(0.05)

[a] $\overline{FI}_F$: cage mean of average daily feed intake on ad libitum feeding; G_F average daily growth on ad libitum feeding; M_F: metabolic body weight on ad libitum feeding
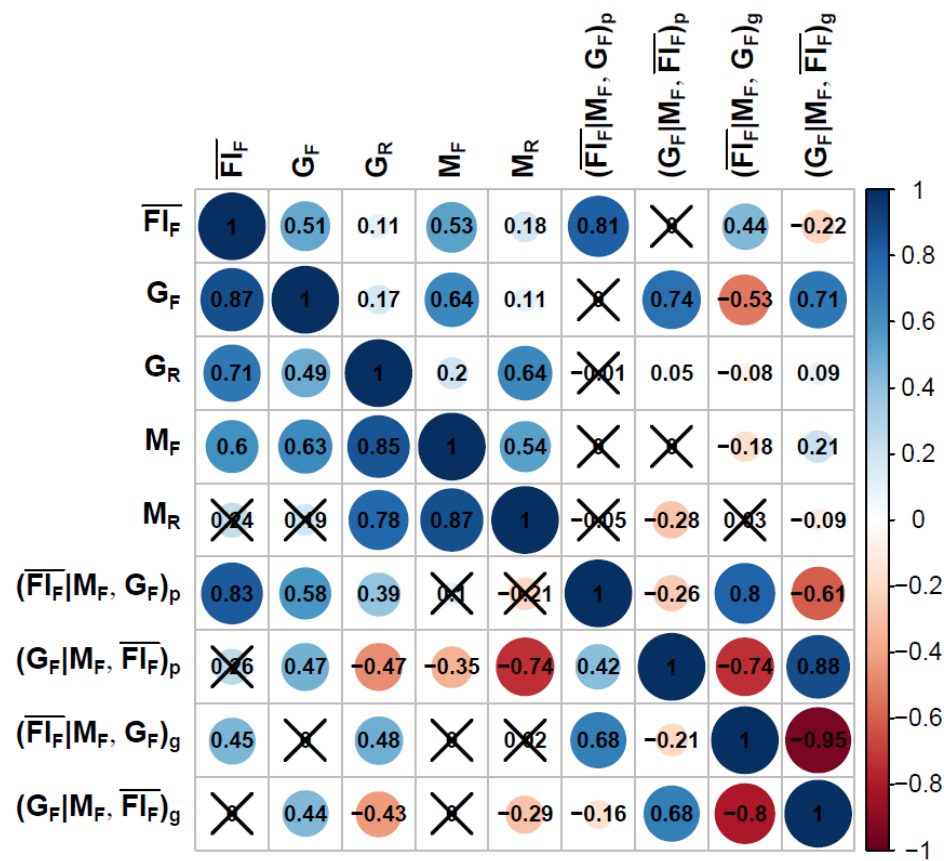[b] h^2: heritability; l^2: litter variance relative to phenotypic variance

Figure 1. Genetic (Lower Triangular) and Phenotypic (Upper Triangular) correlations between selection indexes representing different conditional and unconditional traits. Cells with a cross have a posterior probability of being greater or smaller than zero lower than 0.95.