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 ($\overline{\mathbf{FI}}_{\mathbf{F}}$) and individual records of growth rate ($\mathbf{G}_{\mathbf{F}}$) and metabolic weight ($\mathbf{M}_{\mathbf{F}}$). Growth rate ($\mathbf{G}_{\mathbf{R}}$) 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, $\mathbf{M}_{\mathbf{R}}$) 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 $\overline{\mathrm{FI}}_{\mathrm{F}}|\mathrm{M}_{\mathrm{F}}, \mathrm{G}_{\mathrm{F}}$ and $\mathrm{G}_{\mathrm{F}}|\mathrm{M}_{\mathrm{F}}, \overline{\mathrm{FI}}_{\mathrm{F}}$ were obtained from elements of additive genetics ($\left(\overline{\mathrm{FI}}_{\mathrm{F}}|\mathrm{M}_{\mathrm{F}}, \mathrm{G}_{\mathrm{F}}\right)_g$ and $\left(\mathrm{G}_{\mathrm{F}}|\mathrm{M}_{\mathrm{F}}, \overline{\mathrm{FI}}_{\mathrm{F}}\right)_g$) or phenotypic ($\left(\overline{\mathrm{FI}}_{\mathrm{F}}|\mathrm{M}_{\mathrm{F}}, \mathrm{G}_{\mathrm{F}}\right)_p$ and $\left(\mathrm{G}_{\mathrm{F}}|\mathrm{M}_{\mathrm{F}}, \overline{\mathrm{FI}}_{\mathrm{F}}\right)_p$) (co)variance matrices. In the first case, heritabilities were low (0.07 and 0.06 for $\left(\overline{\mathrm{FI}}_{\mathrm{F}}|\mathrm{M}_{\mathrm{F}}, \mathrm{G}_{\mathrm{F}}\right)_g$ and $\left(\mathrm{G}_{\mathrm{F}}|\mathrm{M}_{\mathrm{F}}, \overline{\mathrm{FI}}_{\mathrm{F}}\right)_g$, 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 $\left(\overline{\mathrm{FI}}_{\mathrm{F}}|\mathrm{M}_{\mathrm{F}}, \mathrm{G}_{\mathrm{F}}\right)_p$ and

$\left(G_F|M_F,\overline{FI}_F\right)_p$, respectively) but the genetic correlation between $\left(\overline{FI}_F|M_F,G_F\right)_p$ and G_F was moderate (0.58). Heritability of G_R was low (0.08). This trait was negatively correlated with $\left(G_F|M_F,\overline{FI}_F\right)_p$ and $\left(G_F|M_F,\overline{FI}_F\right)_g$ of animals on F, which indicate a different genetic background. The correlation between G_R and G_F was also low to moderate (0.48) and the additive variance of G_F was almost 4 times that of G_R, suggesting the presence of a substantial genotype by feeding regimen interaction.

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

Introduction

Despite economic and environmental importance of improving feed efficiency (**FE**) (Kennedy et al., 1993; Shirali et al., 2012), direct selection for this trait has not been performed in most breeding programs in rabbit mainly because of the problems associated with individual recording of feed intake (**FI**). Indirect selection for average daily gain (**G**) or weight at the end of the growing period has been performed instead (Rochambeau, 1989; Estany et al., 1992; Luckefahr et al., 1996; Piles and Blasco, 2003). However, genetic correlation between those traits and FE may not be high enough to result in a significant correlated response (Piles et al. 2004). Therefore, alternative direct selection procedures must be found. Recently, selection for increased G on restricted feeding (**G_R**) has been proposed as selection criteria to improve FE since variation in this trait is directly related to variation in FE because of constant FI (Nguyen et al., 2005). Selection for this trait is expected to yield a greater response on FE than selection for increased average daily gain under full-feeding (**G_F**). Other approaches involve the measurement of individual FI, like selection for residual feed intake (RFI) defined as the difference between actual FI and that predicted from a phenotypic fixed (Koch et al., 1963) or random (Piles et al., 2007; Aggrey and Rekaya, 2013; Sánchez et al., 2017; Shirali et al., 2017) regression of FI on requirements for production and maintenance of body condition. When RFI is calculated at

phenotypic level, there is no phenotypic correlation between residuals (RFI) and the explanatory variables representing animal's needs, but this does not guarantee null genetic correlations. In fact, unfavourable genetic response on growth has been observed after selection for RFI calculated from phenotypic regressions (Gilbert et al., 2007; Cai et al., 2008; Drouilhet et al. 2016). This result was previously shown by Kennedy et al. (1993) who proposed basing the correction of FI not on the phenotypic regression, but on the genetic regression of FI on production traits. They defined "restricted residual feed intake" (**RRFI**), because of its equivalence to a restricted selection index in which production traits are held constant. This definition of RRFI guarantees null genetic correlation with performance traits, and thus null correlated response on them. However, expected direct response would be lower than that of selection based on phenotypic regression (i.e. RFI). Implementation of this definition of FE has been performed using multiple-trait models for individual records of FI (Strathen et al. 2014; Shirali et al., 2018). Only Shirali et al. (2015) used group records of FI to estimate genetic parameters of the classical definition of RFI using a single-trait model with different (but correlated) genetic and permanent effects for each cage mate, which could be considered a different approach. The opportunity of using group records is important because measurement of FI at the group level is feasible and cheaper than individual recording due to the expensive equipment required (Su et al., 2018).

In this paper we propose and discuss the use of selection criteria to improve FE of animals housed in groups and fed ad libitum (**F**). Those definitions of FE involve the use of group records of FI and individual records of growth and body weight. In addition, we estimate genetic parameters of G_R and the magnitude of genotype by feeding regimen interaction on FE traits.

Material and Methods

Animals and experimental design

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

a rabbit sire line selected for G_F during the fattening period (from 32 to 60 d of age). Animals were bred under constant environmental and management conditions from weaning (32 d) to slaughter age (67 d), except feeding regimen which was F or restricted (**R**). After weaning, kits were randomly assigned to one of these two treatments and were grouped according to two classes of body weight: 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 the same litter were distributed between both feeding regimens. A maximum of two kits per litter were allocated to the same cage. Actual feed restriction was on average 75 and 74.1% of the *ad libitum* intake in BS and SS kits, respectively. Individual body weight and cage feed intake were systematically recorded weekly during the whole fattening period. All kits were fed the same pellet diet, supplied once per day in a feeder with three places, and water was always available. Feed was changed to a standard food without antibiotics during the last week of fattening. Data from this period were not included in the analysis to avoid the impact that this change could have on the results. In addition, only data from cages containing the initial 8 kits at the end of the fattening were used for the analysis (667 out of 983 cages). Those data corresponded to 5,336 kits from 101 sires and 423 dams in 1,255 litters produced in 14 batches (between July 2012 and June 2014) and housed in 667 cages. For the whole control period, individual average daily feed intake in cages on F ($\mathbf{\overline{FI}_F}$) was computed for each cage as the regression coefficient of cage cumulated mean FI (i.e. cumulated FI/8) on age in days. Likewise, $\mathbf{G_F}$ and $\mathbf{G_R}$ were computed for each animal as the regression coefficients of its body weight on age in days for F and R, respectively. In addition, metabolic body weight ($\mathbf{M_F}$ and $\mathbf{M_R}$, on F and R, respectively) was computed as the mean of the weekly values computed as the average of individual body weight at the beginning and the end of the corresponding week to the power 0.75.

Statistical Analysis

Variance components for a number of conditional traits reflecting FE were estimated using information from cage records of $\overline{\mathrm{FI}}_{\mathrm{F}}$ and individual records of G_F, M_F, G_R and M_R. A five-trait mixed model was implemented. Model for $\overline{\mathrm{FI}}_{\mathrm{F}}$ can be written as:

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

where, $\overline{\mathrm{FI}}_{\mathrm{F,ijk}}$ is the individual average daily feed intake record of the k[th] cage on F, in the i[th] batch and the j[th] group of size class; $\mathbf{x}'_{\mathrm{POk}}$,$\mathbf{x}'_{\mathrm{LSk}}$, $\mathbf{z}'_{\mathrm{lk}}$, $\mathbf{z}'_{\mathrm{ak}}$ and $\mathbf{z}'_{\mathrm{pk}}$are vectors containing the proportion of animals in the k[th] cage in each level of the factors: parity order, litter size, litter, additive genetic and individual environmental, respectively; the length of those vectors is the number of levels of the corresponding factor. $\mathrm{B_i}$ is the effect of the i[th] batch (14 levels), $\mathrm{S_j}$ is the effect of the j[th] size class (2 levels: BS, SS); **PO** is the vector of parity order effects (4 levels: 1, 2, 3 and >3); **LS** is the vector of litter size effects (7 levels: < 6, 6, 7, 8, 9, 10, > 10); **l** is the vector of litter effects (1,255 levels); **a** is the vector of breeding values (6,531 levels, i.e. animals in the pedigree corresponding to 5 generations); **d** is the vector of individual environmental effects (5,336 levels, i.e. animals with records); $\mathrm{c_k}$ is the effect of the k[th] cage (667 levels) and $\mathrm{e_{ijk}}$ is the residual.

For individually recorded traits (G_F, G_R, M_F and M_R) exactly the same model was used, but now the design vectors $\mathbf{x}'_{\mathrm{POk}}$,$\mathbf{x}'_{\mathrm{LSk}}$, $\mathbf{z}'_{\mathrm{lk}}$, $\mathbf{z}'_{\mathrm{ak}}$ and $\mathbf{z}'_{\mathrm{dk}}$ contained either 0 or 1.

In a Bayesian framework, this model corresponds to the expectation of the distribution of the data given model parameters –conditional likelihood; in our case, a multivariate normal distribution was considered. The systematic effects, $\mathbf{B}$ and $\mathbf{S}$, were assumed *a priori* to follow uniform distributions. The *a priori* distribution of the additive genetic effect was $p(\mathbf{a}|\mathbf{G}) \sim \mathrm{N}(\mathbf{0}, \mathbf{G} \otimes \mathbf{A})$, where $\mathbf{G}$ is the 5 × 5 additive genetic covariance matrix between traits and $\mathbf{A}$ is the numerator relationship matrix, of dimension N, equal to the number of individuals in the pedigree. The *a priori* distribution of litter effects, cage environmental effects and individual environmental effects were $p(\mathbf{l}|\mathbf{L}) \sim \mathrm{N}(\mathbf{0}, \mathbf{L} \otimes \mathbf{I_l})$, $p(\mathbf{c}|\mathbf{C}) \sim \mathrm{N}(\mathbf{0}, \mathbf{C} \otimes \mathbf{I_c})$ and $p(\mathbf{d}|\mathbf{D}) \sim \mathrm{N}(\mathbf{0}, \mathbf{D} \otimes \mathbf{I_d})$, respectively, where $\mathbf{l}$, $\mathbf{c}$ and $\mathbf{d}$ are the corresponding vectors of environmental effects, $\mathbf{L}$, $\mathbf{C}$ and $\mathbf{D}$ are the corresponding 5 × 5 covariance 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 (i.e. 1,303, 667 and 5,336, respectively). Similarly, the distribution of the residual effects was

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

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

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

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

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

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

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

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

Cage effects on $\overline{\mathrm{FI}}_{\mathrm{F}}$ and environmental individual effects on individually recorded traits are necessary factors to take into account properly the environmental covariance between $\overline{\mathrm{FI}}_{\mathrm{F}}$ and individually recorded traits. If these effects were not considered, part of this environmental covariance could be assigned to genetic covariance. Thus, although these effects would not be identifiable in univariate models they are necessary in a multivariate setting. In this multivariate scenario, covariance between traits allows for the identification of cage effects on $\overline{\mathrm{FI}}_{\mathrm{F}}$ and environmental individual effects on individually recorded traits (G_F, G_R, M_F and M_R), but given that the amount of information to separate them from the residual effects is limited, total environmental variance was defined as the addition of cage, individual environmental and residual variance components ($\mathbf{E} = \mathbf{C} + \mathbf{D} + \mathbf{R}$) in each sampling iteration. Samples of elements of **R** matrix related to $\overline{\mathrm{FI}}_{\mathrm{F}}$ were previously multiplied by 8 (i.e. the number of animals in a cage) to rescale them to variation at individual level, instead of mean level. Finally, total phenotypic variance matrix was defined as $\mathbf{P} = \mathbf{G} + \mathbf{L} + \mathbf{E}$

Phenotypic and genetic RFI definitions are equivalent to selection indexes based on the component traits with weights equal to the corresponding partial regression coefficients at a negative value (Kennedy et al, 1993). Phenotypic and genetic variance-covariance matrices for those selection indexes were defined as was shown by Kennedy et al. (1993) and recently implemented by Shirali et al. (2018): $\boldsymbol{I_G} = \boldsymbol{b}'\boldsymbol{G}\boldsymbol{b}$ and $\boldsymbol{I_P} = \boldsymbol{b}'\boldsymbol{P}\boldsymbol{b}$. In our case, $\boldsymbol{b}$ matrix is composed of 5 columns, one for each original trait, and 9 rows. The first five rows correspond to indexes only involving the original traits. The following two rows correspond to indexes which are equivalent to conditional traits with respect to the phenotypic variance-covariance matrix, and the last two rows correspond to indexes which are equivalent to conditional traits with respect to the genetic variance-covariance matrix. These two sets of either phenotypic or genotypic conditional traits correspond to feed intake conditional on growth and metabolic weight under full feeding ($\overline{\mathrm{FI}}_{\mathrm{F}}|\mathrm{G}_{\mathrm{F}}, \mathrm{M}_{\mathrm{F}}$) (i.e. residual feed intake, Kennedy et al., 1993) and growth conditional on feed intake and metabolic weight, all of them on full feeding ($\mathrm{G}_{\mathrm{F}}|\overline{\mathrm{FI}}_{\mathrm{F}}, \mathrm{M}_{\mathrm{F}}$) (i.e. residual growth, Crowley et al., 2010). As indicated by Kennedy et al. (1993), conditioning with

respect to the distribution of genetic effects ($\left(\overline{\mathbf{FI}}_{\mathbf{F}}\middle|\mathbf{G}_{\mathbf{F}},\mathbf{M}_{\mathbf{F}}\right)_{\mathbf{g}}$ and $(\mathbf{G}_{\mathbf{F}}|\overline{\mathbf{FI}}_{\mathbf{F}},\mathbf{M}_{\mathbf{F}})_{\mathbf{g}}$) would guarantee a null genetic correlation between conditioned and conditioning traits. When the conditional is effected with respect to the phenotypic distribution of the recorded traits ($\left(\overline{\mathbf{FI}}_{\mathbf{F}}\middle|\mathbf{G}_{\mathbf{F}},\mathbf{M}_{\mathbf{F}}\right)_{\mathbf{p}}$ and $(\mathbf{G}_{\mathbf{F}}|\overline{\mathbf{FI}}_{\mathbf{F}},\mathbf{M}_{\mathbf{F}})_{\mathbf{p}}$), the phenotypic correlation between those traits is null but the genetic correlation is not guaranteed to be so.

In order to illustrate the computation of each row of the **b** matrix, we present the cases for $\left(\overline{\mathrm{FI}}_{\mathrm{F}}\middle|\mathrm{G}_{\mathrm{F}},\mathrm{M}_{\mathrm{F}}\right)_{\mathrm{g}}$ and $\left(\overline{\mathrm{FI}}_{\mathrm{F}}\middle|\mathrm{G}_{\mathrm{F}},\mathrm{M}_{\mathrm{F}}\right)_{\mathrm{p}}$, assuming that the order of the traits in the covariance matrix is $\overline{\mathrm{FI}}_{\mathrm{F}}$, G_{F}, G_{R}, M_{F} and M_{R}.

For the case in which the conditional is effected with respect to the additive genetic effects distribution of the recorded traits, the b matrix is:

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

Where $\mathrm{b}_{\mathrm{g;FI_F|G_F}}$ and $\mathrm{b}_{\mathrm{g;FI_F|}M_{\mathrm{F}}}$ are computed as

$$\begin{bmatrix}\mathrm{b}_{\mathrm{g;FI_F|G_F}}\\ \mathrm{b}_{\mathrm{g;FI_F|}M_{\mathrm{F}}}\end{bmatrix} = \begin{bmatrix}\sigma_{\mathrm{g;FI_F,G_F}} & \sigma_{\mathrm{g;FI_F,M_F}}\end{bmatrix}\begin{bmatrix}\sigma^2_{\mathrm{g;G_F}} & \sigma_{\mathrm{g;G_F,M_F}}\\ \sigma_{\mathrm{g;G_F,M_F}} & \sigma^2_{\mathrm{g;M_F}}\end{bmatrix}^{-1};$$

When the conditional is effected with respect to the phenotypic distribution of the recorded traits, the b matrix is:

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

Where $\mathrm{b}_{\mathrm{p;FI_F|G_F}}$ and $\mathrm{b}_{\mathrm{p;FI_F|}M_{\mathrm{F}}}$ were computed as

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

The adopted Bayesian MCMC framework is the optimal to characterize the posterior distributions of the variance-covariance matrix involving the described conditional traits, i.e. selection indexes. Single chains of 1,000,000 iterations were run discarding the first 200,000. Samples of the parameters of interest were saved every 100 rounds. Samples from the marginal posterior distributions of the variance components of the defined selection indexes, at genetic ($\boldsymbol{I_G = b'Gb}$) and at phenotypic ($\boldsymbol{I_P = b'Pb}$) levels, were obtained in each round of the Gibbs sampler.

Results

Table 1 shows summary statistics of the analysed traits. As expected, growth mean was larger for animals on F than R because of the limited amount of food provided to animals on R. However, variation was slightly higher for G_R than for G_F (the coefficients of variation were 0.17 and 0.21 on F and R, respectively).

All variance components were higher for animals on F than for animals on R, particularly the phenotypic variance for G, which was 1.5 times larger for animals on F than for animals on R (63.34 vs 44.08) . The heritability was nearly three times larger for G_F than for G_R (posterior mean 0.21 vs 0.08), but the ratio of phenotypic variance due to litter effects was higher on R than F (Table 2). With regard to the environmental variance –the sum of cage, individual environment, and residual variances - relative to the phenotypic variance, a larger effect was observed for G_R than for G_F (posterior mean [posterior s.d.]: 0.75 [0.03] vs 0.67 [0.04]). The differences between M_R and M_F for variance components were much smaller than those observed between G_R and G_F. Thus, in both metabolic weight traits heritability was around 0.35, being the ratio of litter effect variance to phenotypic variance around 0.25. Cage average feed intake showed a heritability of 0.32. For this trait, litter

effects played a much smaller role, the ratio of litter effect variance relative to phenotypic variance being just 0.07.

Differences in genetic variances and genetic correlation lower than 1 indicates the existence of genotype by feeding regimen interaction. For G, the genetic correlation (Table 3 and Figure 1) was just 0.49 [0.15] while for M this correlation was 0.87 [0.04], clearly showing that the magnitude of the interaction between the genotype and feeding regimen is much larger for growth rate than for metabolic weight. Within each feeding regimen, the genetic correlations between G and M were moderate to high, being the estimates 0.63 [0.09] on F and 0.78 [0.08] on R. The genetic correlations of $\overline{\mathrm{FI}}_{\mathrm{F}}$ with G_F and M_F were moderate to high (0.87 [0.06] and 0.60 [0.12], respectively) whereas it was moderate (0.70 [0.9]) with G_R and low (0.24 [0.15]) with M_R.

The pattern of litter effect correlations (Table 3) was slightly different to that observed for the genetic correlations. For example, the posterior mean [posterior s.d.] of litter effect correlation between growth across the two feeding regimens was 0.73 [0.11], indicating that the interaction between litter effects and feeding regimen was smaller than the interaction between the genotype and feeding regimen. Within each feeding regimen, the litter effect correlations between growth and metabolic weight were 0.35 [0.09] and 0.47 [0.07] on F and R, respectively. Litter effect correlations of $\overline{\mathrm{FI}}_{\mathrm{F}}$ with other traits were null for growth on both feeding regimens and high (above 0.8) with metabolic body weight on both feeding regimens also

The environmental correlation could only be estimated for the traits recorded on the same feeding regimen, because there were no individual records taken on the two alternative feeding regimens. The environmental correlation between G_F and M_F and between G_R and M_R were both moderate to high (0.79 [0.03] and 0.75 [0.02], respectively). The environmental correlation of $\overline{\mathrm{FI}}_{\mathrm{F}}$ with G_F and M_F were moderate, (0.47 [0.11] and 0.45 [0.10], respectively).

Table 4 shows mean and standard deviation of marginal posterior distributions of variance components and ratios of phenotypic variance for different conditional traits. When the conditional is based on the distribution of the additive genetic effects, the heritability is lower than the corresponding to the conditional on the phenotypic distribution of the recorded traits. The estimated value for $\left(\overline{\mathrm{FI}}_{\mathrm{F}} \mid \mathrm{M}_{\mathrm{F}}, \mathrm{G}_{\mathrm{F}}\right)_{\mathrm{p}}$ was 0.22 [0.08] while that for $\left(\overline{\mathrm{FI}}_{\mathrm{F}} \mid \mathrm{M}_{\mathrm{F}}, \mathrm{G}_{\mathrm{F}}\right)_{\mathrm{g}}$ was only 0.07 [0.04]. Similarly, for RG traits the heritability estimates were 0.16 [0.04] and 0.06 [0.03] for $\left(\mathrm{G}_{\mathrm{F}} \mid \mathrm{M}_{\mathrm{F}}, \overline{\mathrm{FI}}_{\mathrm{F}}\right)_{\mathrm{p}}$ and $\left(\mathrm{G}_{\mathrm{F}} \mid \mathrm{M}_{\mathrm{F}}, \overline{\mathrm{FI}}_{\mathrm{F}}\right)_{\mathrm{g}}$, respectively.

As expected, the estimated genetic correlations between conditional traits effected on the distribution of additive genetic effects, and the conditioning traits is null (Figure 1). When the conditional is based on the phenotypic distribution of the traits, these genetic correlations between $\left(\overline{\mathrm{FI}}_{\mathrm{F}} \mid \mathrm{M}_{\mathrm{F}}, \mathrm{G}_{\mathrm{F}}\right)_{\mathrm{p}}$ and G_{F} and M_{F} were 0.58 and 0.10, respectively, and 0.26 and -0.35 between $\left(\mathrm{G}_{\mathrm{F}} \mid \mathrm{M}_{\mathrm{F}}, \overline{\mathrm{FI}}_{\mathrm{F}}\right)_{\mathrm{p}}$ and $\overline{\mathrm{FI}}_{\mathrm{F}}$ and M_{F}, respectively. The genetic correlations between residual growth and RFI traits are very different depending on whether genetic or phenotypic distributions were used for conditioning. In the first case, a high and negative genetic correlation (-0.8) was obtained while in the second case, the correlation was moderate and positive (0.42, Figure 1). Within type-of-efficiency trait, i.e. residual growth or RFI, the genetic correlation between definitions based on genetic or phenotypic conditioning was, in both cases, 0.68. The estimated genetic correlations between conditional feed efficiency traits and G_{R} followed the same pattern regardless of conditioning based on phenotypic or genetic relationships between traits. It was low to moderate and positive with RFI traits (0.39 with $\left(\overline{\mathrm{FI}}_{\mathrm{F}} \mid \mathrm{M}_{\mathrm{F}}, \mathrm{G}_{\mathrm{F}}\right)_{\mathrm{p}}$ and 0.48 with $\left(\overline{\mathrm{FI}}_{\mathrm{F}} \mid \mathrm{M}_{\mathrm{F}}, \mathrm{G}_{\mathrm{F}}\right)_{\mathrm{g}}$), and low to moderate but negative with residual growth traits (-0.47 with $\left(\mathrm{G}_{\mathrm{F}} \mid \mathrm{M}_{\mathrm{F}}, \overline{\mathrm{FI}}_{\mathrm{F}}\right)_{\mathrm{p}}$ and -0.43 with $\left(\mathrm{G}_{\mathrm{F}} \mid \mathrm{M}_{\mathrm{F}}, \overline{\mathrm{FI}}_{\mathrm{F}}\right)_{\mathrm{g}}$)

Discussion

In this study we have reported variance components and genetic parameters of several measurements of feed efficiency obtained from a model that combines group/cage records of FI and individual records of G and M, under two different feeding regimens commonly applied in rabbit meat production farms. This procedure overcomes difficulties for identification of genetic and environmental random effects of FI when group records are used, as was discussed by Su et al. (2018). In addition, it takes advantage of the definition of FE traits as selection indexes that can be obtained from multiple-trait genetic evaluations (Kennedy et al, 1993). The proposed model includes several random factors of variation such as additive genetic, litter, cage and individual environmental effects. They can be identified due to the genetic and environmental correlation between cage FI and individually recorded production traits. Kennedy et al. (1993) showed that selection based on the traditional RFI definition would yield direct response on efficiency at the expense of a reduction in growth and production traits. To overcome this issue, they defined RRFI as RFI based on genotypic regression rather than on phenotypic regression. Selecting for RRFI, direct response would be lower than that achieved by selection on RFI but no unwanted correlated response on growth would be expected. In our study, we clearly confirm these theoretical results. Thus, for our population, we can 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 FE of the animals. On the contrary, the selection for increasing $\left(G_F \mid M_F, \overline{FI}_F\right)_p$ or reducing $\left(\overline{FI}_F \mid M_F, G_F\right)_p$ will improve FE, but at the expense of an increase in FI and a reduction in G, respectively. As noted by Kennedy et al (1993) heritability is generally higher for RFI than for RRFI because heritability of RRFI is the proportion of the variance of FI which is genetically independent of production. From an applied perspective, the increase in FI could be achieved more easily than the reduction in G. Thus, based on our results, it could be recommended to focus on residual growth rather than on RFI. Another alternative could be to use breeding value predictions for $\left(G_F \mid M_F, \overline{FI}_F\right)_p$ 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

restriction on G_F and $\overline{FI}_F$. Nevertheless, this procedure would yield similar results, in terms of 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 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 relevant to observe that the genetic correlation between them is negative and strong (-0.8). This indicates different biological processes involved in both FE definitions. $\overline{FI}_F|M_F, G_F$ would be related to processes involving the limitation of energy and nutrient resource wastage, whereas $G_F|M_F, \overline{FI}_F$ would be related to metabolic pathways involved in the efficacy of using those acquired resources for 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 positive, which is a consequence of $\left(\overline{FI}_F \mid M_F, G_F\right)_p$ not being genetically independent from $\mathbf{G_F}$.

Direct selection for FE is difficult and expensive to implement because it requires feed intake recording. The ideal situation would be to record FI at individual level, even when the animals are raised in groups. This can be achieved in species, like pigs and cattle, for which automatic recording feeding systems are available. However, this is not yet the case in rabbit production, so direct selection for FE has been conducted until now by recording feed intake in a small proportion of selection candidates raised in individual cages (Drouilhet et al., 2016). This strategy could limit the progress of genetic selection for FE because of the low accuracy of genetic evaluation of FE for most selection candidates, many of which do not have their own records. In this selected population, heritability of RFI has been reported to be 0.16 (Drouilhet et al., 2013). To our knowledge, no estimates of heritability for RG in rabbit have been reported in the literature.

Even in the situation in which electronic feeders are available, it is interesting to explore other sources of information which are less expensive than FI records obtained with them, as it could be FI recorded at the group level (Su et al., 2018). Several studies have reported models for the estimation of genetic parameters and variance components of FI using group data (Olson et al., 2006; Biscarini et al. 2008;

Cooper et al., 2010; Su et al., 2018; Shirali et al., 2018) but only Shirali et al. (2015) combine individual records of production traits and group records of FI in a single-trait model defining phenotypic RFI from a phenotypic regression model of cage FI on body weight of each of the two cage mates. This situation is similar to ours but in our case, given that groups are larger (8 cage mates), the number of available cage records is limited (321). Thus, these records by themselves include a limited amount of information and the consideration of information from correlated traits recorded individually, growth and metabolic weights, is mandatory in order to obtain reliable estimations and predictions from the cage-record model. Therefore, our procedure allows us to obtain predictions of breeding values for phenotypic and genetic definitions of RFI proposed by Kennedy et al. (1993) from a multiple-trait model combining individual and cage records., which has never been performed before

Feed efficiency measurements when animals are raised under restricted feeding

Selection for G_R has been proposed as a strategy to select for FE (Nguyen & McPhee 2005, Nguyen et al., 2005). When animals are raised individually and under feed restriction, so that the same amount of feed is provided to all the animals, their growth represents a direct measurement of FE. In those conditions, variation in growth is directly related to variation in FE because of constant FI (Nguyen et al., 2005) and therefore, individual records of FI are not required. This is partially equivalent to the definition of $\mathrm{G_F}|\mathrm{M_F}, \overline{\mathrm{FI}}_\mathrm{F}$ if the role of $\mathrm{M_F}$ is ignored. When the animals are raised in collective cages, which is our case, within-cage variation in FI might exist, and the meaning of G_R as a FE trait is not clear. The magnitude of the genetic correlations with FE traits defined for animals raised on F could aid to our understanding of the value of G_R as a FE trait.

Genetic variance and heritability (0.08) of G_R for animals raised in groups were both low. Therefore, it would be difficult to achieve a positive response to selection for this trait when the animals are raised in collective cages. In addition, G_R seems to be only moderately correlated to any FE trait on F and the sign of those correlations is the opposite to the ones expected between the different measures of FE

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 1). The reason to expect opposite signs in the estimated correlations is related to the observed 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 defined by conditioning on the phenotypic or on the genetic covariance matrix. Therefore, based on these results it seems that G_R of animals in groups seems not to be linked to any biological process involved in FE, at least to those definitions of FE on F. Piles et al (2017) have shown that social genetic effects contribute substantially to total genetic merit of rabbits raised on R when collective cages are used. Models accounting for these indirect genetic effects have shown that the correlation between these effects and direct genetics effects is negative when animals are fed on R. Thus, the existence of this negative correlation could explain the observed correlation between G_R and feed efficiency definitions on F. This unfavourable genetic correlation between direct and indirect genetic effects greatly compromise the success, in terms of response to selection, of any selection process considering G_R on animals raised in collective cages.

Genotype by feeding regimen interaction

Feed restriction during the first two or three weeks of the growth period has become a common practice in commercial farms because of its positive effect on animal health in the presence of diseases that cause digestive disorders (Gidenne et al., 2012). With this practice, farmers also take advantage of an improved efficiency in the use of feed, mainly as a consequence of the compensatory growth that is observed at the end of the growing period when rabbits are fed on F. If the animals in the nucleus are selected on F but are raised on R in rabbit commercial farms, genetic gain achieved in a breeding program for improving FE could not be transferred to production farms due to the effect of a potential interaction between the genotype and the feeding regimen on this trait. We have estimated variance components and genetic parameters of different measures of FE for animals fed on different feeding regimens. Our results support the idea that G_R and G_F or FE on F are traits with different genetic backgrounds, since the genetic correlation between them is not high (0.48 between

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 between G_R and $G_F|M_F, \overline{FI}_F$ Figure 1). On the other hand, additive genetic variance of G_F is almost 4 times the genetic variance of G_R. The different genetic variances and a genetic correlation lower than 1 clearly indicate the existence of genotype by feeding regimen interaction (Kolmodin 2003). Therefore, if commercial farms produce young rabbits on R, it would be necessary to evaluate which selection procedure yields the highest response in the production farms: selection for G_R, taking into account indirect effects despite its low variability and heritability, or selection on G_F clearly subject to a strong genotype by feeding regimen interaction, but having a large variability and heritability.

In conclusion, group records of FI and individual records of production traits can be jointly used for selection to improve FE. Measurements of FE on R and F in animals raised in groups are correlated at a low level indicating that the magnitude of the genotype by feeding regimen interaction is important, probably as a consequence of the existence of substantial indirect genetic effects especially when animals are on R. In addition, selection for increased G_R could be ineffective at improving FE because of its low heritability on those housing conditions.

Declarations

Ethics approval and consent to participate

The research protocol was approved by the animal care and use committee of the Institut de Recerca i Tecnologia Agroalimentàries (IRTA).

Availability of data and material

The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests

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446

Table 1. Summary statistics

Trait	Abbreviation	N	Mean	sd
Cage Mean Average Daily Feed Intake on Ad libitum feeding	$\overline{\mathrm{FI}}_{\mathrm{F}}$	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	$\overline{\mathbf{FI}}_{\mathbf{F}}$[a]	$\mathbf{G}_{\mathbf{F}}$[a]	$\mathbf{G}_{\mathbf{R}}$[a]	$\mathbf{M}_{\mathbf{F}}$[a]	$\mathbf{M}_{\mathbf{R}}$[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)
$\mathbf{h^2}$[b]	0.32 (0.09)	0.21 (0.05)	0.08 (0.02)	0.38 (0.06)	0.33 (0.05)
$\mathbf{l^2}$[b]	0.07 (0.01)	0.12 (0.02)	0.17 (0.02)	0.24 (0.03)	0.26 (0.03)

[a] $\overline{\mathrm{FI}}_{\mathrm{F}}$: 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

	$\overline{\mathbf{FI}}_{\mathbf{F}} - \mathbf{G}_{\mathbf{F}}$	$\overline{\mathbf{FI}}_{\mathbf{F}} - \mathbf{G}_{\mathbf{R}}$	$\overline{\mathbf{FI}}_{\mathbf{F}} - \mathbf{M}_{\mathbf{F}}$	$\overline{\mathbf{FI}}_{\mathbf{F}} - \mathbf{M}_{\mathbf{R}}$	$\mathbf{G}_{\mathbf{F}} - \mathbf{G}_{\mathbf{R}}$	$\mathbf{G}_{\mathbf{F}} - \mathbf{M}_{\mathbf{F}}$	$\mathbf{G}_{\mathbf{F}} - \mathbf{M}_{\mathbf{R}}$	$\mathbf{G}_{\mathbf{R}} - \mathbf{M}_{\mathbf{F}}$	$\mathbf{G}_{\mathbf{R}} - \mathbf{M}_{\mathbf{R}}$	$\mathbf{M}_{\mathbf{F}} - \mathbf{M}_{\mathbf{R}}$
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] $\overline{\mathrm{FI}}_{\mathrm{F}}$: 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	$\left(\overline{\mathbf{FI}}_{\mathbf{F}} \mid \mathbf{M}_{\mathbf{F}}, \mathbf{G}_{\mathbf{F}}\right)_{\mathbf{p}}$ [a]	$\left(\mathbf{G}_{\mathbf{F}} \mid \mathbf{M}_{\mathbf{F}}, \overline{\mathbf{FI}}_{\mathbf{F}}\right)_{\mathbf{p}}$ [a]	$\left(\overline{\mathbf{FI}}_{\mathbf{F}} \mid \mathbf{M}_{\mathbf{F}}, \mathbf{G}_{\mathbf{F}}\right)_{\mathbf{g}}$ [a]	$\left(\mathbf{G}_{\mathbf{F}} \mid \mathbf{M}_{\mathbf{F}}, \overline{\mathbf{FI}}_{\mathbf{F}}\right)_{\mathbf{g}}$ [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)
$\mathbf{h^2}$ [b]	0.22(0.08)	0.16(0.04)	0.07(0.04)	0.06(0.03)
$\mathbf{l^2}$ [b]	0.08(0.03)	0.29(0.04)	0.21(0.05)	0.25(0.05)

[a] $\overline{\mathrm{FI}}_{\mathrm{F}}$: 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

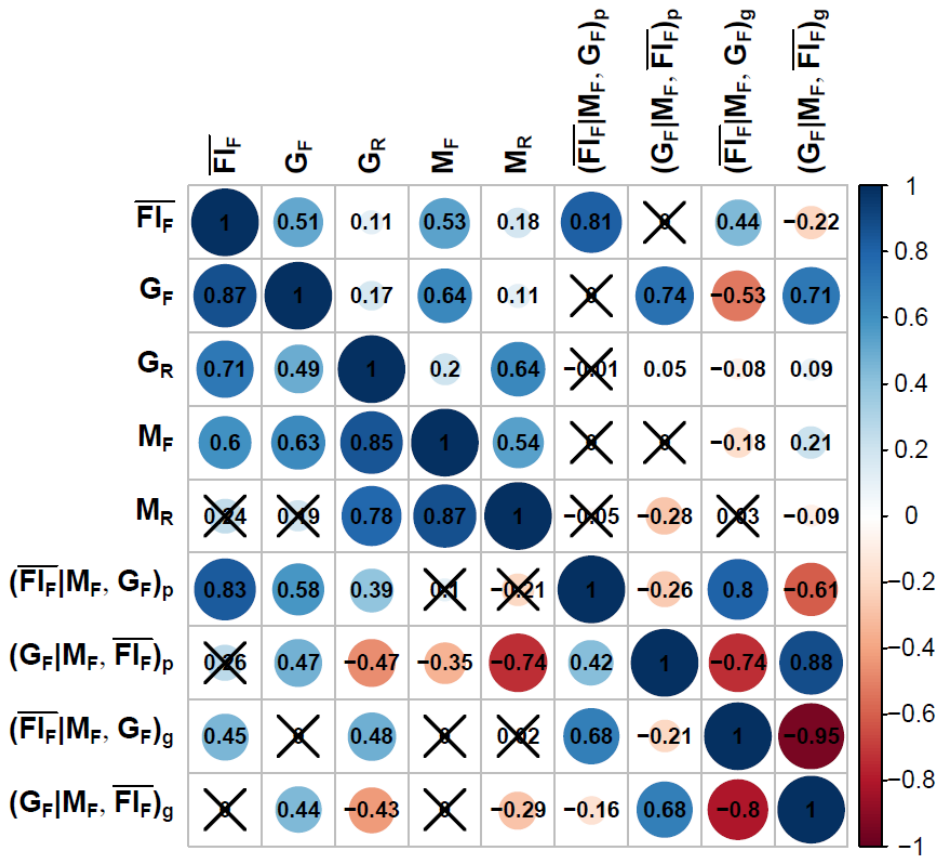

Figure 1. Genetic (Lower Triangular) and Phenotypic (Upper Triangular) correlations between selection indexes representing different conditional and unconditional traits. Cells with a cross have a posterior probability of being greater or smaller than zero lower than 0.95.