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# Different ways to model biological relationships between fertility and pH of the semen in rabbits<sup>1</sup>

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**ABSTRACT:** This work aimed to study the relationship between pH of the semen and fertility (Fert, defined as the success or failure of conception), which is of special interest because pH of the semen can be considered a global marker of the expression of some seminal quality traits. Different methods used to model the relationship between Fert and pH are presented here: 1) ignoring genetic and environmental correlations and including pH either as a covariate or as a cross-classified effect on fertility, 2) a bivariate mixed model, and 3) recursive bivariate mixed models. A total of 653 pH records and 6,365 Fert records after AI were used. Crossbreed does from 2 maternal lines were artificially inseminated with buck semen from a paternal line in a commercial environment. A negative, and almost linear, effect of pH on Fert was detected. The posterior median of pH and Fert heritabilities, and the highest posterior density interval at 95% (in parentheses) were approximately 0.18 (0.05, 0.29) and approximately 0.10 (0.02, 0.20) across all the models, respectively. Genet-

ic correlations between traits were negative, but the highest posterior density interval at 95% included zero [i.e.,  $-0.31$  ( $-0.91, 0.33$ ) in the bivariate mixed model and  $-0.17$  ( $-0.99, 0.48$ ) and  $-0.44$  ( $-0.99, 0.10$ ) in the recursive bivariate mixed models including pH as a covariate or as a cross-classified effect, respectively]. All models predicted Fert data reasonably well (i.e., 76 and 62% correct predictions for success and failure, respectively). No differences in the prediction of the EBV for male fertility were encountered between models, showing a good concordance in the animals ranked by their EBV (the correlation between EBV in all models was close to 1). Thus, no differences in results were obtained considering, or not considering, genetic and environmental correlations between pH and Fert and assuming, or not assuming, recursiveness between each trait. This is because the magnitude of the effect of pH on Fert was not large enough; therefore, the same results were obtained even though the models were of different complexity.

**Key words:** (co)variance component, fertility, pH of semen, rabbit, recursive model

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## INTRODUCTION

Male fertility (**Fert**) is one of the most economically interesting traits in rabbit breeding, especially with the use of AI (Alvaríño, 2000). However, because of the low heritability of this trait in both natural and AI mating systems (Piles et al., 2005; Tusell et al., 2010), finding seminal quality traits to be used as criteria for indirect selection to increase male Fert has been paramount (More O’Ferrall and Meacham, 1968; Bencheikh, 1995; Brun et al., 2002; Lavara et al., 2005). The hydrogen-ion concentration in semen (pH) is a by-product of sperm metabolism associated with the number and activity of spermatozooids. Thus, it can be considered an indicator of seminal quality traits (More O’Ferrall and Meacham, 1968; Bencheikh, 1995); therefore, it is of special interest to determine its relationship to Fert.

Fertility and pH have a complex biological relationship. The pH of semen could affect the phenotypical

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expression of Fert but, contrary to some environmental effects (e.g., type of extender, AI technician, farm), pH is not an external effect of the animal, so, in turn, pH could also have genetic and permanent effects. Recursive models can accommodate this kind of biological relationship.

A recursive multitrait model is a particular case of structural equation models, which Gianola and Sorensen (2004) applied in a quantitative genetic context. These models are useful in describing biological relationships between traits that have simultaneity or recursiveness between their phenotypes, leading to a better interpretation of results. Gianola and Sorensen (2004) also pointed out that, in the presence of feedback and recursiveness, biased (co)variance estimates can be obtained if these relationships are not taken into account. Since then, several authors have been using these models to describe biological relationships between several traits in livestock species (de los Campos et al., 2006; López de Maturana et al., 2007; Varona et al., 2007; Wu et al., 2008).

In this work, we studied the relationship between semen pH and male Fert by using different models: 1) ignoring genetic and environmental correlations between each trait, 2) a classical multitrait model, and 3) recursive multitrait models. Models were compared according to their ability to predict Fert and the across-model EBV correlations. Ratios for genetic and environmental sources of variation were also estimated for both pH and Fert.

## MATERIALS AND METHODS

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

### *Animals and Experimental Design*

Bucks came from the Caldes line, selected for growth rate during the fattening period (Gómez et al., 2002). They were bred and reared on an experimental farm from the Institut de Recerca i Tecnologia Agroalimentàries in Caldes de Montbui (Barcelona, Spain). After weaning at 32 d, males were housed in cages of 8 individuals with a photoperiod of 16 h of light/d. Animals were fed a commercial diet ad libitum (15.5% CP, 2.3% fat, 17.2% fiber; DM basis) until d 60. After this period, they were individually housed and feed was restricted to 180 g/d of another commercial diet (16% CP, 4.3% fat, 17% fiber; DM basis). Fresh water was always available. All males began the training to an artificial vagina at 4.5 mo of age. One ejaculate per male and per week was collected for 2 wk. Their reproductive life began at 5 mo. At this age, 2 ejaculates per male and per week were collected, with an interval of 30 min between collections. From 5 to 9 mo of age, all males were evaluated at 3 different times for seminal quality

traits and Fert score after AI of crossbred females on a commercial farm.

All semen evaluations and preparations of the AI doses were performed in a laboratory located beside the experimental farm of the Caldes line. Ejaculates were stored in a dry bath at 35°C until evaluation, for no more than 15 min after collection. Ejaculates containing urine and calcium carbonate deposits were discarded, and gel plugs were removed. Individual motility of the ejaculate was measured in aliquots (25 µL) under a light microscope (Nikon, Lewisville, TX) at 400× magnification according to a subjective scale from 0 to 5 (0, 1, 2, 3, 4, or 5 = 0 to 10, <10 to 25, <25 to 50, <50 to 70, <70 to 90, or <90 to 100, respectively, of the motile spermatozoa showing progressive movement). A small preselection of ejaculates was performed, discarding for AI only those with individual motility scores less than 2 and a percentage of dead spermatozoa greater than 50%.

Semen pH was determined using a 507 Crison pH meter (Crison Instruments, SA, Barcelona, Spain). Preselecting good-quality ejaculates could have biased the sample. However, most of the rejections (60.5%) were due to the presence of urine or calcium carbonate deposits from the bladder, which are not part of a normal ejaculate and could also affect the pH measurement. Semen was immediately prediluted 1:1 with a commercial extender (Cunigel, IMV Technologies France, L'Aigle, France). The semen from each buck obtained on the same day was pooled, and cell sperm concentration was measured by using a sperm cell counter (NucleoCounter SP-100, ChemoMetec A/S, Allerød, Denmark). The resultant pool was divided into 2 parts, which were diluted to  $10 \times 10^6$  and  $40 \times 10^6$  spermatozoa/mL, respectively, to obtain AI doses at 2 different sperm concentrations. Semen doses were stored in straws of 0.5 mL at 18°C for 24 h until their use.

Artificial insemination was performed on crossbred does [P × V; V line: Estany et al., 1989; P (Prat) line: Gómez et al., 1996] on a commercial farm. Females followed a semi-intensive reproductive rhythm: first mating at about 4.5 mo of age, with subsequent 42-d reproductive cycles. All females were treated 48 h before AI with 15 IU of eCG (subcutaneously; Foligon, Intervet International B.V., Booxmeer, the Netherlands), and ovulation was induced immediately after AI with 0.02 mg of gonadorelin (intramuscularly; Fertagyl, Intervet International B.V., Booxmeer, the Netherlands).

### *Data*

Diagnosis of pregnancy was made by palpation, 14 d after AI, confirming the result at parity. The assigned Fert score was 1 when the female was diagnosed as pregnant and 0 otherwise. A total of 6,613 Fert records, involving 243 males and 2,293 females, were obtained between November 2006 and July 2007. Different Fert records had the same pH measurement. From the to-

tal amount of data, Fert records without a corresponding pH measurement were not included in the analysis, leading to a final figure of Fert data of 6,363.

The pH was measured separately in each ejaculate and pooled whenever 2 ejaculates per male and day were obtained, as follows:

$$pH = -\log_{10} \left[ \frac{10^{-pH_1} \times Vol_1 + 10^{-pH_2} \times Vol_2}{(Vol_1 + Vol_2)^{-1}} \right],$$

where  $pH_1$ ,  $Vol_1$ ,  $pH_2$ , and  $Vol_2$  are pH and volume measures for the first and the second ejaculate of the pool of each male, respectively. To increase the accuracy of the estimates concerning pH, 223 pH data values without Fert results coming from 96 additional males were also incorporated into the analyses. These data were obtained between June 2006 and October 2006 as described above, but with the first and second ejaculate pooled before measuring pH. Thus, from the final 653 pH records, 490 had a paired Fert record.

### Model and Statistical Analysis

Semen pH was assumed to be normally distributed and was analyzed jointly with Fert in a bivariate Gaussian-threshold model (Foulley et al., 1983). In a threshold model, the observed Fert  $y_{Fert}$  is considered the expression of an underlying continuous variable  $l$ , often called the liability (Falconer, 1965), which is rendered discrete by a fixed threshold that divides the observed response into 2 categories (Wright, 1934): the failure or the success of conception. The probability that an observed Fert data value ( $y_{i,Fert}$ ) falls into 1 of these 2 categories given the liability is

$$p(y_{i,Fert} | l_i) = p(l_i > 0)I(y_{i,Fert} = 1) + p(l_i \leq 0)I(y_{i,Fert} = 0).$$

The threshold being fixed at 0,  $I(\cdot)$  is an indicator function that takes the value of 1 or 0.

A bivariate recursive model postulates that trait 1 has an effect on trait 2, but that trait 2 has no effect on trait 1. In the case of recursiveness (but not for simultaneity), the model presented by Gianola and Sorensen (2004) can be expressed as a classical multitrait model in which trait 1 is included as a systematic effect in the model for trait 2 (López de Maturana et al., 2007). In this work, pH is trait 1 and Fert is trait 2. Thus, in our case, the  $j$ th pair of records for an individual  $i$  had the following linear relationship:

$$\begin{pmatrix} y_{ij,pH} \\ l_{ij,Fert} \end{pmatrix} = \begin{pmatrix} \mathbf{x}'_{ij,pH} & 0 \\ 0 & \mathbf{x}'_{ij,Fert} \end{pmatrix} \begin{pmatrix} \boldsymbol{\beta}_{pH} \\ \boldsymbol{\beta}_{Fert} \end{pmatrix} + \begin{pmatrix} 0 & 0 \\ 0 & y_{ij,pH} \end{pmatrix} \begin{pmatrix} 0 \\ \lambda_{Fert \leftarrow pH} \end{pmatrix} + \begin{pmatrix} u_{i,pH} \\ u_{i,Fert} \end{pmatrix} + \begin{pmatrix} pm_{i,pH} \\ pm_{i,Fert} \end{pmatrix} + \begin{pmatrix} 0 \\ pf_{m,Fert} \end{pmatrix} + \begin{pmatrix} pmd_{ij,pH} \\ pmd_{ij,Fert} \end{pmatrix} + \begin{pmatrix} e_{ij,pH} \\ e_{ij,Fert} \end{pmatrix}. \quad [1]$$

The coefficient  $\lambda_{Fert \leftarrow pH}$  denotes the phenotypical rate of change of the liability of Fert with respect to pH (i.e., it models the recursive effect of pH on Fert). The different  $\lambda_{Fert \leftarrow pH}$  assumed in the models were always estimated as systematic effects in Eq. [1]. The terms  $y_{ij,pH}$  and  $l_{ij,Fert}$  were the  $j$ th data value for the observed pH and the unobserved liability for male  $i$ . The term  $\boldsymbol{\beta}_{pH}$  was the vector of systematic effects affecting pH, including day of ejaculate collection (27 levels) and male age (4 levels at about 1 mo intervals from 5 to 9 mo old). The term  $\boldsymbol{\beta}_{Fert}$  was the vector of systematic effects for Fert, including concentration of the AI dose (2 levels: 10 or 40 million spermatozoa/mL), physiological status of the female (3 levels: nulliparous does, multiparous does in lactation, and multiparous does not in lactation at AI), a combined effect between day and inseminator (19 levels at 14-d intervals between November 2006 and July 2007), and a combined effect between the age of the male and the building (9 levels, about 1 mo intervals from 5 to 9 mo of age combined with the 2 buildings on the commercial farm where AI was performed). The term  $\mathbf{x}_{ij,k}$  ( $k = pH, Fert$ ) was the corresponding row of an incidence matrix relating data with systematic effects. The term  $u_{i,k}$  was the male genetic additive effect,  $pm_{i,k}$  was the male permanent environmental effect,  $pf_{m,Fert}$  was the  $m$ th female effect for the Fert trait,  $pmd_{ij,k}$  was the permanent environmental effect resulting from the combination between male and day of AI, and  $e_{ij,k}$  was the random residual effect. Note that for pH,  $pmd_{ij,pH}$  is also a residual component, and it can be separated from the residual only because it is related to  $pmd_{ij,Fert}$  of the Fert model. This residual decomposition increases the data connectivity and permits the estimation of a possible environmental correlation between the traits.

A Bayesian approach was adopted for inference. Note that  $\boldsymbol{\Omega} = \{\boldsymbol{\beta}, \lambda_{Fert \leftarrow pH}, \mathbf{u}_m, \mathbf{p}_m, \mathbf{p}_f, \mathbf{p}_{md}, \mathbf{G}, \mathbf{P}_m, \mathbf{P}_f, \mathbf{P}_{md}, \mathbf{R}\}$  is the vector including all the unknown parameters in the model. The term  $\boldsymbol{\beta}$  is the vector of systematic effects,  $\mathbf{u}_m$  is the vector of male genetic additive effects,  $\mathbf{p}_m$  is the vector of the male nonadditive genetic plus permanent environmental effects,  $\mathbf{p}_f$  is the vector of female effects, and  $\mathbf{p}_{md}$  is the vector of permanent environmental effects resulting from the combination between male and day on which the AI was performed. The terms  $\mathbf{G}$ ,  $\mathbf{P}_m$ ,  $\mathbf{P}_f$ , and  $\mathbf{P}_{md}$  are the different (co)variance matrices of the corresponding random effects defined above, and  $\mathbf{R}$  is the residual (co)variance matrix. The joint posterior distribution of all parameters was

$$\begin{aligned} p(\boldsymbol{\Omega}, \mathbf{1} | \mathbf{y}_{pH}, \mathbf{y}_{Fert}) &\propto p(\mathbf{y}_{pH} | \boldsymbol{\Omega}) \\ &\times p \prod_{i=1}^n \{p(l_i > 0)I(y_i = 1) + p(l_i \leq 0)I(y_i = 0)\} \\ &\times p(\mathbf{1} | \boldsymbol{\Omega}) \times p(\boldsymbol{\Omega}). \end{aligned}$$

The prior distributions for the parameters of the model were  $p(\boldsymbol{\beta}) \sim k$ ;  $p(\mathbf{u}_m | \mathbf{G}) \sim N(\mathbf{0}, \mathbf{A} \otimes \mathbf{G})$ ;  $p(\mathbf{p}_m | \mathbf{P}_m)$



**Table 1.** Summary statistics of the cross-classified effect of pH (1 to 8) included in the fertility model

| Item                     | 1    | 2          | 3             | 4             | 5            | 6            | 7          | 8       |
|--------------------------|------|------------|---------------|---------------|--------------|--------------|------------|---------|
| Range                    | ≤7   | (>7, 7.13) | (>7.13, 7.25) | (>7.25, 7.38) | (>7.38, 7.5) | (>7.5, 7.75) | (>7.75, 8) | (>8, 9) |
| Mean                     | 6.80 | 7.06       | 7.19          | 7.31          | 7.44         | 7.60         | 7.88       | 8.21    |
| No. of fertility records | 796  | 710        | 915           | 1,074         | 881          | 1,001        | 601        | 387     |

–  $N(\mathbf{0}, \mathbf{I} \otimes \mathbf{P}_m)$ ;  $p(\mathbf{p}_f | \mathbf{P}_f) - N(\mathbf{0}, \mathbf{I} \otimes \mathbf{P}_f)$ ;  $p(\mathbf{p}_{md} | \mathbf{P}_{md}) - N(\mathbf{0}, \mathbf{I} \otimes \mathbf{P}_{md})$ ; and  $p(\mathbf{e} | \mathbf{R}) - N(\mathbf{0}, \mathbf{I} \otimes \mathbf{R})$ , where  $k$  is a constant and  $\mathbf{A}$  is the numerator relationship matrix. Bounded uniform prior distributions were assumed for  $\beta$ ,  $\lambda_{Fert \leftarrow pH}$ , and the components of  $\mathbf{G}$ ,  $\mathbf{P}_m$ ,  $\mathbf{P}_f$ ,  $\mathbf{P}_{md}$ , and  $\mathbf{R}$ . The  $\mathbf{R}$  was a diagonal matrix with the residual variance for Fert set to 1. Data augmentation was used to deal with the missing Fert data (Sorensen and Gianola, 2002).

Three sets of models to describe the pH and Fert relationship were used. Within each model, different types of  $\lambda_{Fert \leftarrow pH}$  were assumed (i.e., null, covariate, or cross-classified effect) to accommodate null, linear and nonlinear recursive effects (López de Maturana et al., 2009) of pH on Fert. Table 1 shows the summary statistics for the different levels of  $\lambda_{Fert \leftarrow pH}$  as a cross-classified effect in the Fert model.

### Univariate Mixed Models

In the univariate mixed models (**UMM**), the genetic and environmental correlations between each trait were set to zero. This implies that the phenotypic recursion is the only cause of correlation between any of the random effects (López de Maturana et al., 2010). The effect of pH on Fert ( $\lambda_{Fert \leftarrow pH}$ ) was estimated as a covariate in the **UMM<sub>cov</sub>** model or as a cross-classified effect of 8 categories (as described in Table 1) in the **UMM<sub>cross</sub>** model.

### Bivariate Mixed Model

In the bivariate mixed model (**BMM**), the 2 traits were genetically and environmentally correlated. In the **BMM<sub>0</sub>** model, the genetic and environmental relationships between each trait were accounted for by the covariances and no recursive effect was assumed ( $\lambda_{Fert \leftarrow pH} = 0$ ).

### Bivariate Recursive Mixed Models

To take into account the phenotypical influence of pH on Fert, and also the genetic and environmental relationships between each trait, 2 recursive Gaussian-threshold (mixed) models (**RMM**) were proposed. First, model **RMM<sub>cov</sub>** had  $\lambda_{Fert \leftarrow pH}$  as a covariate. Some identification problems appeared in this model. Because the  $\mathbf{p}_{md}$  effect is also a residual component in the pH model, the restriction that  $\mathbf{P}_{md}$  was diagonal was added to ensure likelihood identification (Varona et al., 2007). Second, model **RMM<sub>cross</sub>** had  $\lambda_{Fert \leftarrow pH}$  as

a cross-classified effect of 8 categories (as described in Table 1). Table 2 shows the type of structural coefficient  $\lambda_{Fert \leftarrow pH}$  and the structure of the (co)variance component matrices used in each of the models.

### The Gibbs Sampler

Procedures developed by Sorensen et al. (1995) and extensions of them, based on Markov chain Monte Carlo methods, allow the univariate and joint analysis of categorical and continuous traits. Marginal posterior distributions of the parameters of interest were approximated using the Gibbs sampler algorithm (using the TM software developed by Legarra et al. 2008). Fully conditional posterior distributions of the model parameters needed for the implementation of this algorithm can be found in Sorensen and Gianola (2002). Single chains of 500,000 iterations were run for all the models, discarding the first 50,000 iterations of each chain and saving 1 of every 10 samples. The number of samples discarded in the burn-in was, in all the analyses, much larger than the value recommended by Raftery and Lewis (1992) and Geweke (1992) for assessing convergence. The sampling variance of the chains was obtained by computing Monte Carlo SE (Geyer, 1992).

### Recursive Model as an Alternative Parameterization of a Classical Bivariate Model

Following Varona et al. (2007), a recursive model can have an equivalent parameterization in a classical bivariate model. This equivalence is as follows:  $\mathbf{\Lambda}^{-1} \mathbf{H}^* (\mathbf{\Lambda}^{-1})' = \mathbf{H}$ , where

$$\mathbf{\Lambda} = \begin{pmatrix} 1 & 0 \\ -\lambda_{Fert \leftarrow pH} & 1 \end{pmatrix}$$

is the matrix of structural coefficients, and  $\mathbf{H}^*$  and  $\mathbf{H}$  are the different (co)variance components of the recursive and the bivariate mixed model, respectively. In our study,  $\mathbf{H}$  corresponded to the  $\mathbf{G}$ ,  $\mathbf{P}_m$ ,  $\mathbf{P}_f$ ,  $\mathbf{P}_{md}$ , and  $\mathbf{R}$  described above, and this equivalence was assessed between the **RMM<sub>cov</sub>** and **BMM<sub>0</sub>** models.

### Data Prediction Ability and EBV Comparison

Posterior predictive distribution of Fert data was calculated in all the models. Thus, the ability to predict

**Table 2.** Structural coefficients ( $\lambda_{Fert \leftarrow pH}$ ) and (co)variance component matrices for the male additive effects ( $\mathbf{G}$ ), the male nonadditive plus permanent environmental effects ( $\mathbf{P}_m$ ), the female effects ( $\mathbf{P}_f$ ), the permanent environmental effects of male and day of AI ( $\mathbf{P}_{md}$ ), and the residual effects ( $\mathbf{R}$ ) for pH of the semen and fertility (Fert) assumed in the different models<sup>1</sup>

| Parameter                      | UMM <sub>cross</sub>   | UMM <sub>cov</sub>   | BMM <sub>0</sub>   | RMM <sub>cross</sub>   | RMM <sub>cov</sub>   |
|--------------------------------|--|--|--|--|--|
| $\lambda_{Fert \leftarrow pH}$ | Cross-classified   | Covariate  | 0  | Cross-classified   | Covariate  |
| $\mathbf{G}$                   | $\begin{pmatrix} \sigma_{u,pH}^2 & 0 \\ 0 & \sigma_{u,Fert}^2 \end{pmatrix}$           | $\begin{pmatrix} \sigma_{u,pH}^2 & 0 \\ 0 & \sigma_{u,Fert}^2 \end{pmatrix}$           | $\begin{pmatrix} \sigma_{u,pH}^2 & \sigma_{u,pH,Fert} \\ \sigma_{u,Fert,pH} & \sigma_{u,Fert}^2 \end{pmatrix}$                     | $\begin{pmatrix} \sigma_{u,pH}^2 & \sigma_{u,pH,Fert} \\ \sigma_{u,Fert,pH} & \sigma_{u,Fert}^2 \end{pmatrix}$                     | $\begin{pmatrix} \sigma_{u,pH}^2 & \sigma_{u,pH,Fert} \\ \sigma_{u,Fert,pH} & \sigma_{u,Fert}^2 \end{pmatrix}$         |
| $\mathbf{P}_m$                 | $\begin{pmatrix} \sigma_{P_m,pH}^2 & 0 \\ 0 & \sigma_{P_m,Fert}^2 \end{pmatrix}$       | $\begin{pmatrix} \sigma_{P_m,pH}^2 & 0 \\ 0 & \sigma_{P_m,Fert}^2 \end{pmatrix}$       | $\begin{pmatrix} \sigma_{P_m,pH}^2 & \sigma_{P_m,pH,Fert} \\ \sigma_{P_m,Fert,pH} & \sigma_{P_m,Fert}^2 \end{pmatrix}$             | $\begin{pmatrix} \sigma_{P_m,pH}^2 & \sigma_{P_m,pH,Fert} \\ \sigma_{P_m,Fert,pH} & \sigma_{P_m,Fert}^2 \end{pmatrix}$             | $\begin{pmatrix} \sigma_{P_m,pH}^2 & \sigma_{P_m,pH,Fert} \\ \sigma_{P_m,Fert,pH} & \sigma_{P_m,Fert}^2 \end{pmatrix}$ |
| $\mathbf{P}_f$                 | $\begin{pmatrix} 0 & 0 \\ 0 & \sigma_{P_f,Fert}^2 \end{pmatrix}$                       | $\begin{pmatrix} 0 & 0 \\ 0 & \sigma_{P_f,Fert}^2 \end{pmatrix}$                       | $\begin{pmatrix} 0 & 0 \\ 0 & \sigma_{P_f,Fert}^2 \end{pmatrix}$   | $\begin{pmatrix} 0 & 0 \\ 0 & \sigma_{P_f,Fert}^2 \end{pmatrix}$   | $\begin{pmatrix} 0 & 0 \\ 0 & \sigma_{P_f,Fert}^2 \end{pmatrix}$   |
| $\mathbf{P}_{md}$              | $\begin{pmatrix} \sigma_{P_{md},pH}^2 & 0 \\ 0 & \sigma_{P_{md},Fert}^2 \end{pmatrix}$ | $\begin{pmatrix} \sigma_{P_{md},pH}^2 & 0 \\ 0 & \sigma_{P_{md},Fert}^2 \end{pmatrix}$ | $\begin{pmatrix} \sigma_{P_{md},pH}^2 & \sigma_{P_{md},pH,Fert} \\ \sigma_{P_{md},Fert,pH} & \sigma_{P_{md},Fert}^2 \end{pmatrix}$ | $\begin{pmatrix} \sigma_{P_{md},pH}^2 & \sigma_{P_{md},pH,Fert} \\ \sigma_{P_{md},Fert,pH} & \sigma_{P_{md},Fert}^2 \end{pmatrix}$ | $\begin{pmatrix} \sigma_{P_{md},pH}^2 & 0 \\ 0 & \sigma_{P_{md},Fert}^2 \end{pmatrix}$                                 |
| $\mathbf{R}$                   | $\begin{pmatrix} \sigma_{e,pH}^2 & 0 \\ 0 & 1 \end{pmatrix}$                           | $\begin{pmatrix} \sigma_{e,pH}^2 & 0 \\ 0 & 1 \end{pmatrix}$                           | $\begin{pmatrix} \sigma_{e,pH}^2 & 0 \\ 0 & 1 \end{pmatrix}$   | $\begin{pmatrix} \sigma_{e,pH}^2 & 0 \\ 0 & 1 \end{pmatrix}$   | $\begin{pmatrix} \sigma_{e,pH}^2 & 0 \\ 0 & 1 \end{pmatrix}$   |

<sup>1</sup>UMM<sub>cross/cov</sub> = mixed model without genetic and environmental correlations for pH and fertility including pH as a cross-classified effect (cross) or as a covariate (cov) in the model of fertility; BMM<sub>0</sub> = bivariate mixed model for pH and fertility; RMM<sub>cross/cov</sub> = recursive mixed model for pH and fertility including pH as a cross-classified effect (cross) or as a covariate (cov) in the model of fertility.

success or failure in each Fert record was averaged as follows:

$$E(\hat{y}_{Fert} | \mathbf{y}_{Fert}, \mathbf{\Omega}, \mathbf{1}, M) = \frac{1}{n} \sum_{i=1}^n (\hat{y}_{Fert,i} | \mathbf{y}_{Fert}, \mathbf{\Omega}_i, \mathbf{1}_i, M),$$

where  $\hat{y}_{Fert}$  is the vector of predicted data on the observed scale,  $\mathbf{y}_{Fert}$  is the observed Fert data,  $\mathbf{\Omega}$  is the vector of unknown parameters,  $\mathbf{1}$  is the vector of liabilities,  $M$  is the model used, and  $n$  is the total number of iterations. Each predicted Fert value was assumed to be correct when the absolute value of the difference between the observed Fert and the posterior mean of the posterior distribution did not differ by more than 0.25. Thus, good data prediction was achieved when the probability of correctly predicting data was  $\geq 75\%$ :

$$y_{Fert,i} - E(\hat{y}_{Fert,i} | \mathbf{y}_{Fert,-i}, \mathbf{\Omega}, \mathbf{1}, M) \leq 0.25.$$

Correlations between the posterior means of the EBV for Fert obtained in the models were calculated to evaluate possible differences in the estimation of male additive genetic effects. The average EBV of the top 10% animals was also calculated in each of the models.

## RESULTS AND DISCUSSION

The average semen pH was 7.43 (SD = 0.42), well within the range of values obtained previously in the same line and in other rabbit breeds (Bencheikh, 1995; Brun et al., 2002; García-Tomás et al., 2006a; Brun et al., 2009). The current Fert (52%) was less than had been observed previously in the nucleus of selection of this paternal line over purebred females when us-

ing either natural mating (86.2%; Piles et al., 2005) or AI (71.7%, Tusell et al., 2010). The AI conditions of this experiment (smaller sperm dosage and 24-h storage period of the doses before AI on a commercial farm over crossbred females) could be more unfavorable than natural mating conditions and the AI conditions in the nucleus of selection over purebred females (high sperm dosage, no storage period). To our knowledge, there is only 1 published research paper reporting Fert results after AI using homospermic doses (Brun et al., 2002). After rejecting a larger number of ejaculates, Brun et al. (2002) obtained similar Fert rates (ranging from 49.4 to 63.6% in 2 purebred lines and their reciprocal crosses). However, female receptivity was not artificially induced and could contribute to reducing Fert even after strong sperm quality selection.

### Effect of Structural Coefficients of pH on Fert

Table 3 shows the estimates on the liability scale of the  $\lambda_{Fert \leftarrow pH}$  effects in each model. Estimates of each level within each cross-classified effect  $\lambda_{Fert \leftarrow pH}$  were obtained as deviations from the estimated marginal posterior distribution (EMPD) of the mean Fert liability. Transformations from the underlying scale to the observed scale of the effects of the structural coefficients on Fert are plotted in Figure 1. The estimated values of  $\lambda_{Fert \leftarrow pH}$  as a covariate or as a cross-classified effect were consistent across all the models, indicating that an increase in pH leads to a decrease in Fert, and this relation seems to be almost linear. The recursive models were the ones that had a shallower slope in this decrease, probably because part of the pH effect was included in the covariances between the random

**Table 3.** Means (SD) of the posterior distributions of the recursive effect of pH in the liability of fertility, with  $\lambda$  and  $\lambda_i$  (for  $i = 1, \dots, 8$ ) as a covariate or as a cross-classified effect

| Model <sup>1</sup>   | $\lambda$    | $\lambda_1$ | $\lambda_2$ | $\lambda_3$ | $\lambda_4$ | $\lambda_5$  | $\lambda_6$  | $\lambda_7$  | $\lambda_8$  |
|----------------------|--------------|-------------|-------------|-------------|-------------|--------------|--------------|--------------|--------------|
| UMM <sub>cross</sub> | —            | 0.42 (0.16) | 0.28 (0.16) | 0.17 (0.15) | 0.08 (0.14) | -0.03 (0.15) | -0.09 (0.14) | -0.41 (0.16) | -0.49 (0.19) |
| UMM <sub>cov</sub>   | -0.63 (0.11) | —           | —           | —           | —           | —            | —            | —            | —            |
| RMM <sub>cross</sub> | —            | 0.19 (0.21) | 0.14 (0.18) | 0.07 (0.16) | 0.03 (0.14) | -0.02 (0.15) | -0.01 (0.15) | -0.25 (0.20) | -0.19 (0.28) |
| RMM <sub>cov</sub>   | -0.15 (0.07) | —           | —           | —           | —           | —            | —            | —            | —            |

<sup>1</sup>UMM<sub>cross/cov</sub> = mixed model for pH and fertility without genetic and environmental correlations including pH as a cross-classified effect (cross) or as a covariate (cov) in the model of fertility; RMM<sub>cross/cov</sub> = recursive mixed model for pH and fertility including pH as a cross-classified effect (cross) or as a covariate (cov) in the model of fertility.

effects of the traits. The observed negative relationship between pH and Fert agrees with previous studies that evidenced a negative correlation between pH of the ejaculate and Fert (Coffey, 1988; Brun et al., 2002) and also with litter size (More O'Ferrall and Meacham, 1968). The greater the concentration and motility of spermatozooids in ejaculates, the lower the pH because of a greater production of lactic acid (Hulet and Ercanbrack, 1962; Coffey, 1988; Bencheikh, 1995; Brun et al., 2002; García-Tomás et al., 2006b). Thus, pH can be an indicator of semen quality, offering AI centers an easy way to select ejaculates and males for AI to improve Fert. Although the relationship between pH and Fert is almost linear, the inclusion of  $\lambda_{Fert \leftarrow pH}$  as a cross-classified effect allows checking nonlinearity without an apparent loss of accuracy or computing problems.

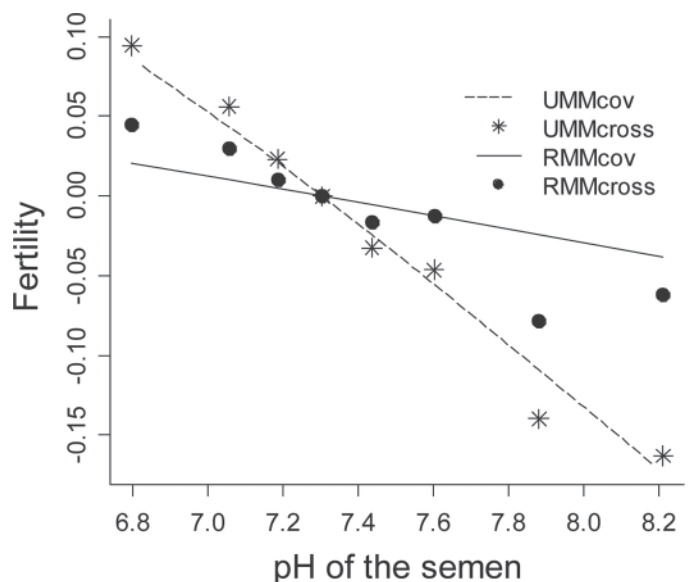
### (Co)Variance Components

Table 4 shows features of the posterior distributions of phenotypic variances, ratios of variances, and correlations between traits. The posterior median of pH heritability ( $h^2$ ) was equal in all the models (0.18) but was greater than had been reported previously (Brun et al., 2009). The difference between the  $h^2$  values could be because in our work the analyzed trait was the pH corresponding to the pooled semen obtained from each male in the day of collection, whereas Brun et al. (2009) used pH measurements from individual ejaculates. Greater  $h^2$  estimates are obtained if the trait consists of means of several records than if it corresponds to an individual record (Ducrocq and Humblot, 1995; Wolf, 2009). The posterior median of pH repeatability ( $r_{pH}$ ) was approximately 0.23, with the highest posterior probability density interval at 95% (HPD<sub>95%</sub>) being approximately [0.13, 0.34] in the models presented. Previous studies in rabbits showed similar values of  $r_{pH}$ : 0.07 to 0.24 by Bencheikh (1995), who compared groups with different frequencies of ejaculate extraction, and 0.17 by Brun et al. (2009). García-Tomás et al. (2006b) obtained an  $r_{pH}$  of 0.38 in 2 paternal lines of rabbits (one of them being the Caldes line) and its reciprocal crosses.

The posterior median of  $h^2$  for male Fert was 0.10, and its repeatability ( $r_{Fert}$ ) was approximately 0.19 with HPD<sub>95%</sub> being approximately [0.12, 0.26] across all the models. Both estimates were greater than had been reported previously (HPD<sub>95%</sub> of  $h^2 = [0.004, 0.024]$ ,  $r_{Fert}$

= 0.044; Piles et al., 2005). The probability of  $h^2 > 0.02$  was greater than 96% in all the models. The AI procedure used in this work (stringent ejaculate selection, reduced spermatic concentration, and use of the doses after a storage period) were probably optimal to detect Fert differences between males (Amann and Hammerstedt, 2002). This fact could lead to obtaining a greater genetic variability of this trait than the one obtained after natural mating. This was probably due to the observation of other genetic effects in underlying Fert that were masked in optimal conditions of AI or after natural mating (Tusell et al., 2010).

Biased trait parameters could be obtained if the selection criterion (growth rate) was correlated with the analyzed traits (Gianola and Fernando, 1986). To our knowledge, these correlations have not been estimated. Nevertheless, genetic correlation between female Fert and growth rate was low (-0.13; Tusell et al. 2009). Because the genetic correlation for male and female Fert seems to be positive in this line (Piles et al., 2005), it is



**Figure 1.** Effect of pH on fertility on the observed scale in the different models for pH of the semen and fertility: a mixed model without genetic and environmental correlations including pH as a covariate or as cross-classified effect in the model of fertility (models UMM<sub>cov</sub> and UMM<sub>cross</sub>, respectively), and recursive mixed models including pH as a covariate or as a cross-classified effect in the model of fertility (RMM<sub>cov</sub> and RMM<sub>cross</sub>, respectively).



**Table 4.** Medians (highest posterior density interval at 95%) of the posterior distributions of the phenotypic variance ( $\sigma^2$ ), phenotypic correlation (r), male heritability ( $h^2$ ), ratios of variance ( $p_i$ ), and correlations ( $r_i$ ) across the different models for semen pH and fertility (Fert)<sup>1</sup>

| Model <sup>2</sup>   | Trait | $\sigma^2$ (diagonal) <sup>3</sup> ;<br>r (above diagonal) | $h^2$ (diagonal);<br>$r_g$ (above diagonal)    | $p_m$ (diagonal);<br>$r_m$ (above diagonal)     | $p_f$                | $p_{md}$ (diagonal);<br>$r_{md}$ (above diagonal)                       |
|----------------------|-------|--|--|---|----------------------|---|
| UMM <sub>cross</sub> | pH    | 0.15<br>(0.13, 0.17)                                       | 0.18<br>(0.07, 0.29)                           | 0.05<br>(0.00, 0.13)                            |                      |   |
|                      | Fert  | 1.67<br>(1.54, 1.82)                                       | 0.10<br>(0.02, 0.20)                           | 0.07<br>(0.00, 0.15)                            | 0.02<br>(0.00, 0.04) | 0.21<br>(0.15, 0.28)  |
| UMM <sub>cov</sub>   | pH    | 0.15<br>(0.13, 0.17)                                       | 0.18<br>(0.07, 0.29)                           | 0.05<br>(0.00, 0.13)                            |                      |   |
|                      | Fert  | 1.66<br>(1.53, 1.80)                                       | 0.10<br>(0.02, 0.20)                           | 0.06<br>(0.00, 0.15)                            | 0.02<br>(0.00, 0.04) | 0.21<br>(0.15, 0.27)  |
| BMM <sub>0</sub>     | pH    | 0.15<br>(0.13, 0.17)                                       | 0.18<br>(0.06, 0.29)                           | 0.05<br>(0.00, 0.14)                            |                      |   |
|                      | Fert  | -0.21<br>(-0.28, -0.14)<br>1.75<br>(1.61, 1.91)            | -0.31<br>(-0.91, 0.33)<br>0.10<br>(0.02, 0.19) | -0.74<br>(-0.99, 0.74)<br>0.09<br>(0.02, 0.17)  | 0.02<br>(0.00, 0.04) | 0.24<br>(0.04, 0.67)<br>-0.57<br>(-0.99, -0.28)<br>0.21<br>(0.16, 0.28) |
| RMM <sub>cross</sub> | pH    | 0.15<br>(0.13, 0.17)                                       | 0.17<br>(0.05, 0.29)                           | 0.04<br>(0.00, 0.14)                            |                      |   |
|                      | Fert  | -0.13<br>(-0.29, 0.03)<br>1.73<br>(1.58, 1.91)             | -0.17<br>(-0.99, 0.48)<br>0.10<br>(0.00, 0.18) | -0.72<br>(-0.99, 0.47)<br>0.09<br>(0.02, 0.18)  | 0.02<br>(0.00, 0.05) | 0.22<br>(0.00, 0.67)<br>-0.34<br>(-0.99, 0.22)<br>0.20<br>(0.15, 0.27)  |
| RMM <sub>cov</sub>   | pH    | 0.15<br>(0.14, 0.17)                                       | 0.17<br>(0.06, 0.29)                           | 0.07<br>(0.00, 0.17)                            |                      |   |
|                      | Fert  | -0.12<br>(-0.19, -0.05)<br>1.71<br>(1.574, 1.87)           | -0.44<br>(-0.99, 0.10)<br>0.10<br>(0.02, 0.19) | -0.89<br>(-0.99, -0.22)<br>0.09<br>(0.03, 0.18) | 0.02<br>(0.00, 0.04) | 0.29<br>(0.00, 0.17)<br>0.19<br>(0.03, 0.18)                            |

<sup>1</sup> $i$  = g (male additive effect), m (environmental plus genetic nonadditive variation attributable to the male), f (variation attributable to the female), and md (environmental variation attributable to the male and day of AI).

<sup>2</sup>UMM<sub>cross/cov</sub> = mixed model for pH and fertility without genetic and environmental correlations including pH as a cross-classified effect (cross) or as a covariate (cov) in the model of fertility; BMM<sub>0</sub> = bivariate mixed model for pH and fertility; RMM<sub>cross/cov</sub> = recursive mixed model for pH and fertility including pH as a cross-classified effect (cross) or as a covariate (cov) in the model of fertility.

<sup>3</sup>Diagonal = the limits of the diagonal are within a set of 2 columns and within a model.

expected that the genetic correlation between male Fert and growth rate is negligible as well.

Although estimates were very imprecise, the posterior median of genetic correlation ( $r_g$ ) between pH and Fert was moderately negative in all the models [i.e.,  $P(r_g < 0)$  of 0.83, 0.68, and 0.91 for  $BMM_0$ ,  $RMM_{cov}$ , and  $RMM_{cross}$ , respectively]. Semen pH is also genetically correlated with several motility parameters that, in turn, are related to Fert (Brun et al., 2002, 2009).

### **Recursive Model as an Alternative Parameterization of a Classical Bivariate Model**

Following the method of Varona et al. (2007), the expression that defines the equivalence for the phenotypic (co)variance components between a recursive and a classical bivariate model is  $\Lambda_{RMM_{cov}}^{-1} \left( \mathbf{V}_{RMM_{cov}} \right) \left( \Lambda_{RMM_{cov}}^{-1} \right)' = \mathbf{V}_{BMM_0}$ . The matrix of structural coefficients containing the regression coefficient of pH on Fert is

$$\Lambda_{RMM_{cov}} = \begin{bmatrix} 1 & 0 \\ -0.15 (0.07) & 1 \end{bmatrix}$$

(Table 3;  $RMM_{cov}$  model). The term  $\mathbf{V}_{RMM_{cov}}$  denotes the phenotypic (co)variance matrix estimated with model  $RMM_{cov}$  (Table 4). Therefore,

$$\Lambda_{RMM_{cov}}^{-1} \left( \mathbf{V}_{RMM_{cov}} \right) \left( \Lambda_{RMM_{cov}}^{-1} \right)' = \begin{bmatrix} 0.15 (0.01) & -0.08 (0.02) \\ -0.08 (0.02) & 1.74 (0.08) \end{bmatrix}.$$

These values are almost equal to the phenotypic (co)variance matrix obtained with the  $BMM_0$  model:

$$\mathbf{V}_{BMM_0} = \begin{bmatrix} 0.15 (0.01) & -0.11 (0.02) \\ -0.11 (0.02) & 1.76 (0.08) \end{bmatrix}.$$

### **Model Comparison**

The ability to predict Fert data was similar across all the models: 76% of correctly predicted successes and 62% of correctly predicted failures. Figure 2 shows the histograms of the mean of posterior predictive distributions for success and failure Fert data estimated using models  $UMM_{cov}$ ,  $BMM_0$ , and  $RMM_{cross}$ .

Correlations between posterior means of the EBV for male Fert across models were close to 1. No differences were encountered in the average EBV of the top 10% animals among the models. Thus, after performing a truncated selection of the best 10% ranked by its EBV, the same the genetic gain would be obtained by using any of the models studied. The highest correlations

were between models that differed only in the type of  $\lambda_{Fert-pH}$  included in the model (covariate or cross-classified effect), confirming the linear effect of pH on Fert.

Despite differing in complexity, the models did not differ in terms of Fert predictions. This was due to both the imprecision of parameter estimation and the low magnitude of those parameters.

### **Effect of AI Dose Concentration and Physiological Status of the Female on Fert**

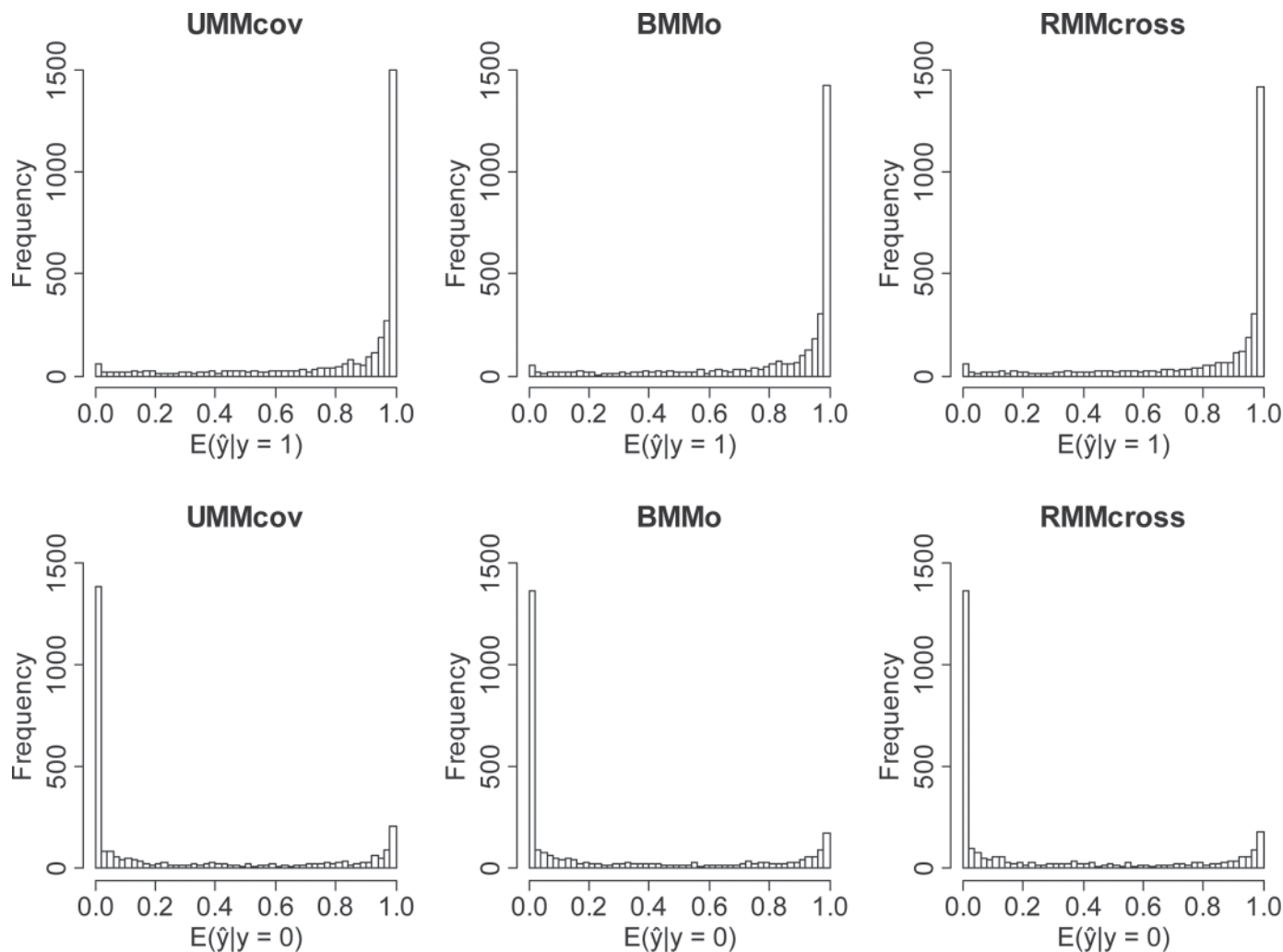
For simplicity, only results from model  $UMM_{cov}$  are presented. The amount of sperm per dose had an important effect on Fert. The EMPD of differences in Fert percentage between AI at 40 or  $10 \times 10^6$  spermatozoa/mL was 10.0 (HPD<sub>95%</sub> = [8.0, 11.8]). It is known that increasing the concentration can compensate for some seminal deficiencies associated with low Fert (Farrell et al., 1993; Alvarino et al., 1996; Viudes-de-Castro and Vicente, 1997; Saacke et al., 2000).

Lactation had a negative effect on Fert. The EMPD of differences in Fert percentage between lactating and nonlactating females was  $-5.2$  HPD<sub>95%</sub> =  $[-8.1, -2.5]$ . This result agrees with previous estimates obtained after natural mating in the same line (Piles et al., 2005) and in another breed in which receptive and lactating females had a smaller kindling rate than the ones not in lactation (Brun et al., 2002). Lactation produces decreases in female receptivity, ovulation rate, and ovulation frequency, and also increases in the number of embryo deaths and postimplantation mortality (Théau-Clément and Roustan, 1992; Fortun and Bolet, 1995). Although, in this work, ovulation was hormonally induced, some negative effects of lactation on female Fert had not been totally suppressed.

### **Conclusions**

There is a quasi-linear negative effect of semen pH on Fert in rabbits. This effect could be equally estimated by using either recursive or classical multivariate models. Both types of models predicted Fert data reasonably well. No differences in the prediction of the EBV for male Fert were encountered between models, showing a good concordance when the animals were ranked by their EBV and in their average EBV of the top 10% best animals. Thus, from the point of view of selection, irrespective of the model of choice, small changes would be encountered in the evaluation of the animal for male Fert. The fact that the models were almost equivalent despite differing in complexity may have been due to small recursiveness effect of pH on Fert and the low precision obtained for the parameter estimates.

The pH of semen could be used to select qualitatively better ejaculates to increase Fert. However, despite the moderate value of heritability obtained for this trait, it does not seem to be advisable to use semen pH as a selection criterion to improve male Fert by indirect



**Figure 2.** Posterior predictive distributions of data on the mean of a fertility success [ $E(\hat{y}|y = 1)$ ] and the mean of a fertility failure [ $E(\hat{y}|y = 0)$ ] estimated in the following models for fertility and pH of the semen: a mixed model without genetic and environmental correlations including pH as a covariate in the model of fertility (model  $UMM_{cov}$ ), a bivariate mixed model ( $BMM_0$ ), and a recursive mixed model including pH as a cross-classified effect in the model of fertility ( $RMM_{cross}$ ).

selection because the genetic correlation between the 2 traits might not be sufficiently high.

## LITERATURE CITED

- Alvariño, J. M. R. 2000. Reproductive performance of male rabbits. Pages 13–35 in Proc. 7th World Rabbit Congr. A. Universidad Politécnica de Valencia, Valencia, Spain.
- Alvariño, J. M. R., F. J. López, J. A. Del Arco, R. Bueno, and R. Torres. 1996. Effects of semen concentration on rabbit artificial insemination with fresh or 24 hours stored semen. Pages 33–35 in Proc. 6th World Rabbit Congr. 2. Association Française de Cuniculture, Lempdes, France.
- Amann, R. P., and R. H. Hammerstedt. 2002. Detection of differences in fertility. *J. Androl.* 23:317–325.
- Bencheikh, N. 1995. The effect of frequency of ejaculation on semen characteristics and sperm output in the rabbit. *Ann. Zootech.* 44:263–279.
- Brun, J. M., A. Sanchez, R. Duzert, G. Saleil, and M. Theau-Clément. 2009. Paramètres génétiques des caractéristiques de la semence de lapin. 13èmes J. Rech. Cunicole (Le Mans, France) 11:17–18.
- Brun, J. M., M. Theau-Clement, and G. Bolet. 2002. The relationship between rabbit semen characteristics and reproductive performance after artificial insemination. *Anim. Reprod. Sci.* 70:139–149.
- Coffey, D. S. 1988. Androgen action and the sex accessory tissues. Pages 108–119 in *Physiology of Reproduction*. E. Knobil and J. D. Neill, ed. Raven Press, New York, NY.
- de los Campos, G., D. Gianola, P. Boettcher, and P. Moroni. 2006. A structural equation model for describing relationships between somatic cell score and milk yield in dairy goats. *J. Anim. Sci.* 84:2934–2941.
- Ducrocq, V., and P. Humblot. 1995. Genetic characteristics and evolution of semen production of young Normande bulls. *Livest. Prod. Sci.* 41:1–10.
- Estany, J., M. Baselga, A. Blasco, and J. Camacho. 1989. Mixed model methodology for the estimation of genetic response to selection in litter size of rabbits. *Livest. Prod. Sci.* 21:67–75.
- Falconer, D. S. 1965. The inheritance of liability to certain diseases, estimated from the incidence among relatives. *Ann. Hum. Genet.* 29:51–76.
- Farrell, P. B., R. H. Foote, M. E. Simkin, E. D. Clegg, and R. J. Wall. 1993. Relationship of semen quality, number of sperm inseminated, and fertility in rabbits. *J. Androl.* 14:464–471.
- Fortun, F., and G. Bolet. 1995. Les effets de la lactation sur les performances de reproduction chez le lapine. *INRA Prod. Anim.* 8:49–56.
- Foulley, J. L., D. Gianola, and R. Thompson. 1983. Prediction of genetic merit from data on binary and quantitative variates

- with an application to calving difficulty, birth weight and pelvic opening. *Genet. Sel. Evol.* 15:401–424.
- García-Tomás, M., J. Sanchez, O. Rafel, J. Ramon, and M. Piles. 2006a. Heterosis, direct and maternal genetic effects on semen quality traits of rabbits. *Livest. Sci.* 100:111–120.
- García-Tomás, M., J. Sanchez, O. Rafel, J. Ramon, and M. Piles. 2006b. Variability, repeatability and phenotypic relationships of several characteristics of production and semen quality in rabbit. *Anim. Reprod. Sci.* 93:88–100.
- Geweke, J. 1992. Evaluating the Accuracy of Sampling-Based Approaches to the Calculation of Posterior Moments. Oxford University Press, Oxford, UK.
- Geyer, C. J. 1992. Practical Markov chain Monte Carlo. *Stat. Sci.* 7:473–511.
- Gianola, D., and R. L. Fernando. 1986. Bayesian methods in animal breeding theory. *J. Anim. Sci.* 63:217–244.
- Gianola, D., and D. Sorensen. 2004. Quantitative genetic models for describing simultaneous and recursive relationships between phenotypes. *Genetics* 167:1407–1424.
- Gómez, E. A., O. Rafel, and J. Ramon. 2002. The Caldes strain (Spain). *Options Méditerr. B Études Rech.* 38:193–198.
- Gómez, E. A., O. Rafel, J. Ramon, and M. Baselga. 1996. A genetic study of a line selected on litter size at weaning. Pages 289–292 in *Proc. 6th World Rabbit Congr. 2*, Toulouse, France. Association Française de Cuniculture, Lempdes, France.
- Hulet, C. V., and S. K. Ercanbrack. 1962. A fertility index for rams. *J. Anim. Sci.* 21:489–493.
- Lavara, R., E. Moce, F. Lavara, M. P. V. de Castro, and J. S. Vicente. 2005. Do parameters of seminal quality correlate with the results of on-farm inseminations in rabbits? *Theriogenology* 64:1130–1141.
- Legarra, A., L. Varona, and E. López de Maturana. 2008. TM Threshold Model. Accessed Oct. 31, 2008. <http://snp.toulouse.inra.fr/~alegarra/manualtm.pdf>.
- López de Maturana, E., G. de los Campos, X.-L. Wu, D. Gianola, K. Weigel, and G. J. M. Rosa. 2010. Modeling relationships between calving traits: A comparison between standard and recursive mixed models. *Genet. Sel. Evol.* 42:1. doi:10.1186/1297-9686-42-1.
- López de Maturana, E., A. Legarra, L. Varona, and E. Ugarte. 2007. Analysis of fertility and dystocia in holsteins using recursive models to handle censored and categorical data. *J. Dairy Sci.* 90:2012–2024.
- López de Maturana, E., X.-L. Wu, D. Gianola, K. A. Weigel, and G. J. M. Rosa. 2009. Exploring biological relationships between calving traits in primiparous cattle with a Bayesian recursive model. *Genetics* 181:277–287.
- More O’Ferrall, G. J., and T. N. Meacham. 1968. Relationship between pH, other semen traits and fertility in rabbits. Pages 1279–1281 in *VIth Congr. Int. Reprod. Anim. Insem. Artif.* 2, Paris, France. C. Thibault, Physiologie Animal, INRA, Jouy-en-Josas, France.
- Piles, M., O. Rafel, J. Ramon, and L. Varona. 2005. Genetic parameters of fertility in two lines of rabbits with different reproductive potential. *J. Anim. Sci.* 83:340–343.
- Raftery, A. E., and S. Lewis. 1992. How many iterations in the Gibbs sampler? Pages 763–773 in *Bayesian Statistics 4*. Oxford Univ. Press, New York, NY.
- Saacke, R. G., J. C. Dalton, S. Nadir, R. L. Nebel, and J. H. Bame. 2000. Relationship of seminal traits and insemination time to fertilization rate and embryo quality. *Anim. Reprod. Sci.* 60–61:663–677.
- Sorensen, D., S. Andersen, D. Gianola, and I. Korsgaard. 1995. Bayesian-inference in threshold models using Gibbs sampling. *Genet. Sel. Evol.* 27:229–249.
- Sorensen, D., and D. Gianola. 2002. *Likelihood, Bayesian, and MCMC Methods in Quantitative Genetics*. Springer Science and Business Media LLC, New York, NY.
- Théau-Clément, M., and A. Roustan. 1992. A study on relationships between receptivity and lactation in the doe and their influence on reproductive performances. *J. Appl. Res.* 15:412–421.
- Tusell, L., M. García-Tomás, M. Baselga, R. Rekaya, O. Rafel, J. Ramon, M. López-Bejar, and M. Piles. 2010. Genotype  $\times$  AI conditions interaction for male effect on fertility and prolificacy. *J. Anim. Sci.* 88:3475–3485.
- Tusell, L., O. Rafel, J. Ramon, and M. Piles. 2009. Genetic analysis of fertility and average daily gain in rabbit. Pages 172–172 in *Book of Abstracts of EAAP—60th Annu. Meet. Eur. Fed. Anim. Sci.* 15, Barcelona, Spain. Wageningen Academic Publishers, Wageningen, the Netherlands.
- Varona, L., D. Sorensen, and R. Thompson. 2007. Analysis of litter size and average litter weight in pigs using a recursive model. *Genetics* 177:1791–1799.
- Viudes-de-Castro, M. P., and J. S. Vicente. 1997. Effect of sperm count on the fertility and prolificacy rates of meat rabbits. *Anim. Reprod. Sci.* 46:313–319.
- Wolft, J. 2009. Genetic correlations between production and semen traits in pig. *Animal* 3:1094–1099.
- Wright, S. 1934. An analysis of variability in number of digits in an inbred strain of guinea pigs. *Genetics* 19:0506–0536.
- Wu, X.-L., B. Heringstad, and D. Gianola. 2008. Exploration of lagged relationships between mastitis and milk yield in dairy cows using a Bayesian structural equation Gaussian-threshold model. *Genet. Sel. Evol.* 40:333–357.

**References**

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