MALE CONTRIBUTION TO PROLIFICACY AT EARLY STAGE OF GESTATION

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ABSTRACT

The objective of this research was to assess the male contribution to the number of implanted embryos and embryonic survival in a line selected for ovulation rate for 10 generations. In prolific species, these traits could be considered as fertility measurements because they indicate the number and rate of fertilized ova which are able to initiate the embryo development. Selection was based on the phenotypic value of ovulation rate estimated at day 12 of second gestation by laparoscopy. Traits recorded were ovulation rate (OR) estimated as the number of corpora lutea in both ovaries, implanted embryos (IE) estimated as the number of implantation sites and embryonic survival (ES) calculated as IE/OR. A total of 1,477 records from 900 females were used to analyze OR, whereas 1,081 records were used to analyze IE and ES. The number of animals in the pedigree was 1107. The h^2 of the male contribution to IE and ES were low (0.05 [0.01, 0.10] and 0.07 [0.02, 0.12]). The genetic correlations between all the analyzed traits and also between male and female genetic components of EI and ES were estimated with great imprecision and it was not possible to draw any conclusion about them. As expected, the proportion of variation due to the male non-additive genetic plus permanent environmental effects for IE and ES was almost negligible (0.027 [0.001, 0.058] and 0.031 [0.002, 0.068] for EI and ES, respectively), being the repeatability for male contribution to EI and ES around 8% and 10%, respectively.

Key words: embryo survival, genetic parameters, implanted embryos, male, rabbit

INTRODUCTION

In recent years, the use of artificial insemination (AI) in commercial farms has increased. AI centers depend on the efficiency of fertile dose production. Improving the production of fertile doses through some of its components is difficult because it is necessary to establish which set of seminal characteristics should be measured and what levels of those traits are optimal. An alternative could be genetic improvement of male contribution to fertility and prolificacy which, in turns, implies improving the set of seminal characteristics that are important for obtaining fertile doses. In this case, male contribution to fertility and prolificacy can be considered to be the final expression of the effects of semen quality traits and the interaction among them and with the female (Koops et al. 1995; Foote 2003). Few works have been performed in order to know the possibilities of selection for these traits. In an initial study in rabbits, it was shown that reproductive performance after natural mating had an almost null male contribution at parity (Piles et al., 2006). Similar results were found when AI was performed at high sperm dosage (Tusell et al., 2011). Male contribution to embryo survival at early stages of gestation could be greater than thereafter because prenatal survival at later stages is mainly determined by the doe (Bradford, 1979) and other environmental factors.

The objective of this research was to assess the male contribution to number of implanted embryos and embryonic survival after natural mating.

MATERIALS AND METHODS

Animals and experimental design

Animals belonged to a 10 generation selection experiment for ovulation rate, described by Laborda et al. (2011). Selection was based on the phenotypic value of ovulation rate estimated at day 12 of second gestation by laparoscopy. Implantation in rabbits takes place at d 7 and laparoscopy permits to count implantation sites at d 12 (Santacreu et al. 1990).

Ovulation rate (OR), estimated as the number of corpora lutea in both ovaries, and the number of implanted embryos (IE), estimated as the number of implantation sites, were measured by laparoscopy at d 12 of second gestation. Embryonic survival (ES) was calculated as IE/OR. Females from all generations had a second post mortem measurement of OR; further, females from the 1st to the 5th generation had a second post mortem measurement of IE and ES
A total of 1,477 records from 900 females were used to analyze OR, whereas 1,081 records were used to analyze IE and ES. The number of animals in the pedigree was 1107.

Statistical Analysis

Data were analyzed under a bayesian approach by using a bi-variate Gaussian mixed model. The analysis was performed using the Gibbs2f90 developed by Misztal. The model for OR was:

$$\mathbf{y}_{OR} = \mathbf{X}_{OR}\boldsymbol{\beta}_{OR} + \mathbf{Z}_{1,OR}\mathbf{u}_{f,OR} + \mathbf{Z}_{2,OR}\mathbf{p}_{f,OR} + \mathbf{e}_{OR}$$

Where $\boldsymbol{\beta}_{OR}$ is the vector of systematic effects, $\mathbf{u}_{f,OR}$ is the vector of additive genetic effects of the female, $\mathbf{p}_{f,OR}$, is the vector of maternal permanent environmental effects, and $\mathbf{e}_{OR}$ is the random residual vector. Incidence matrices $\mathbf{X}_{OR}$, $\mathbf{Z}_{1,OR}$, and $\mathbf{Z}_{2,OR}$ relate data to the corresponding systematic, genetic and permanent environmental effects. The systematic effects included in the model were: year-season (31 levels), parity order (4 levels: 2, 3, 4, ≥5) and lactation (2 levels: 1 = lactating, 2=no lactating).

The model assumed for IE and ES was:

$$\mathbf{y}_{IE} = \mathbf{X}_{IE}\boldsymbol{\beta}_{IE} + \mathbf{Z}_{1,IE}\mathbf{u}_{f,IE} + \mathbf{Z}_{2,IE}\mathbf{u}_{m,IE} + \mathbf{Z}_{3,IE}\mathbf{p}_{f,IE} + \mathbf{Z}_{4,IE}\mathbf{p}_{m,IE} + \mathbf{e}_{IE}$$

Where $\boldsymbol{\beta}_{IE}$ is the vector of systematic effects, $\mathbf{u}_{f,IE}$ and $\mathbf{u}_{m,IE}$ are the vectors of female and male additive genetic effects, respectively; $\mathbf{p}_{f,IE}$ and $\mathbf{p}_{m,IE}$ are the vectors of female and male non-additive genetic plus permanent environmental effects, respectively; and $\mathbf{e}_{IE}$ is the vector of residuals. Terms $\mathbf{X}_{IE}$, $\mathbf{Z}_{1,IE}$, $\mathbf{Z}_{2,IE}$, $\mathbf{Z}_{3,IE}$, and $\mathbf{Z}_{4,IE}$ are incidence matrices that relate data to the corresponding systematic, genetic and permanent environmental effects. The systematic effects included in the model were the same as for OR.

The following multivariate normal distributions were assumed *a priori* for random effects:

$$p(\boldsymbol{\beta}) \sim k;\ p(\mathbf{u}\,|\,\mathbf{G}) \sim N(\mathbf{0}, \mathbf{G}\otimes\mathbf{A});\ p(\mathbf{p}_{\mathbf{f}}\,|\,\mathbf{P}_{\mathbf{f}}) \sim N(\mathbf{0}, \mathbf{P}_{\mathbf{f}}\otimes\mathbf{I});\ p\left(\mathbf{p}_{m,IE}\,|\,\sigma^2_{p_{m,IE}}\right) \sim N\left(\mathbf{0}, \sigma^2_{p_{m,IE}}\otimes\mathbf{I}\right);$$

$$p(\mathbf{e}\,|\,\mathbf{R}) \sim N(\mathbf{0}, \mathbf{R}\otimes\mathbf{I})$$

Where: **A** is the relationship matrix,

$$\boldsymbol{\beta}' = \left(\boldsymbol{\beta}'_{OR}, \boldsymbol{\beta}'_{IE}\right);\qquad \mathbf{u}' = \left(\mathbf{u}'_{f,OR}, \mathbf{u}'_{f,IE}, \mathbf{u}'_{m,IE}\right);\qquad \mathbf{p}'_{\mathbf{f}} = \left(\mathbf{p}'_{f,OR}, \mathbf{p}'_{f,IE}\right);$$ and,

$$\mathbf{G} = \begin{bmatrix} \sigma^2_{u_{f,OR}} & \sigma_{u_{f,OR},u_{f,IE}} & \sigma_{u_{f,OR},u_{m,IE}} \\ \sigma_{u_{f,IE},u_{f,OR}} & \sigma^2_{u_{f,IE}} & \sigma_{u_{f,IE},u_{m,IE}} \\ \sigma_{u_{m,IE},u_{f,OR}} & \sigma_{u_{m,IE},u_{f,IE}} & \sigma^2_{u_{m,IE}} \end{bmatrix}\ \mathbf{P}_{\mathrm{f}} = \begin{bmatrix} \sigma^2_{p_{f,OR}} & \sigma_{p_{f,OR},p_{f,IE}} \\ \sigma_{p_{f,IE},p_{f,OR}} & \sigma^2_{p_{f,IE}} \end{bmatrix},\ \mathbf{R} = \begin{bmatrix} \sigma^2_{\mathbf{e}_{OR}} & \sigma_{\mathbf{e}_{OR},\mathbf{e}_{IE}} \\ \sigma_{\mathbf{e}_{IE},\mathbf{e}_{OR}} & \sigma^2_{\mathbf{e}_{IE}} \end{bmatrix}$$

Bounded uniform priors were assumed for the systematic effects and the (co)variance components (**G**, $\mathbf{P}_{\mathbf{f}}$, $\sigma^2_{p_{m,IE}}$ and **R**). A single chain of 2,000,000 iterations was run. The first 200,000 iterations of each chain were discarded, and samples of the parameters of interest were saved for each of 20 iterations.

RESULTS AND DISCUSSION

The mean of OR, IE and ES were 15.8, 12.5 and 0.78 respectively. The posterior mean (**PM**) and the interval of 95% of highest posterior density ([**HPD95%**]) of the phenotypic variance for OR, IE and ES were 6.05 [5.56, 6.54], 14.38 [13.07, 15.75] and 0.047 [0.043, 0.052], respectively. These results agree with previous estimates reported in other maternal lines (Brun et al., 1992; García and Baselga, 2002).

The PM [HPD95%] of the h^2 for OR was moderate 0.16 [0.07, 0.26] (figure 1). This result also agrees with previous estimates of this parameter in other maternal lines of rabbits (Blasco et al., 1993; Bolet at al., 1994) and with results obtained from the same set of data with different models (Laborda et al., 2011).

In rabbits, embryonic survival comprises the period from ovulation to implantation (day 7 of gestation). Failures on fertilization or embryogenesis lead to a decrease in embryonic survival and number of implanted embryos. Part of the failures at early stages of gestation is due to seminal characteristics (Saacke et al., 2000). Thus, differences among males for their contribution to IE and ES would be due to variation in the presence of seminal deficiencies which prevent the sperm access to the ova, or in the ability to maintain the fertilization process or subsequent embryogenesis once initiated. Results indicate that the h^2 of the male contribution to IE and ES was low (0.05 [0.01, 0.10] and 0.07 [0.02, 0.12]), respectively. However, it was higher than the male contribution to prolificacy at parity probably because the male contribution at early stages of gestation is not masked by the effect of the doe and the environmental factors through gestation. Piles et al. (2006) found that male contribution to prolificacy at parity (genetic plus permanent environmental effects) was only around 1% in three maternal lines of rabbit. The h^2 of the female contributions to IE and ES was low as well, as reported by Laborda et al., (2012), being the PM [HPD95%]: 0.10 [0.03, 0.18] and 0.10 [0.02, 0.16], respectively.

Male contribution to the number of implanted embryos and embryonic survival could be higher than the one estimated in the present analysis. Firstly, after natural mating, sperm dosage excess the threshold needed to fertilize a large rate of ova and only differences among males in seminal traits that are independent of sperm dosage can be observed, (Tusell et al., 2010); therefore, individual variation among males for IE and ES could be better observed from data obtained from does artificially inseminated under limited AI conditions. Secondly, laparoscopy was only performed on those females that were pregnant at 12 day of gestation. Therefore, individual variation for male and female contributions to the number of implanted embryos and embryo survival could be partly biased, leading to low estimates of this parameter.

The genetic correlation between the female contributions to OR and IE was moderate and favorable (0.59 [0.18, 1.00]); therefore, a correlated response in IE was observed (Laborda et al., 2012). However the genetic correlations between OR and the female contribution to ES, between OR and male contribution to IE and ES, and between female and male contributions to IE and ES were all estimated with great imprecision and it is not possible to draw any conclusion about them. There are no previous published estimates of these parameters in rabbits or other prolific species.

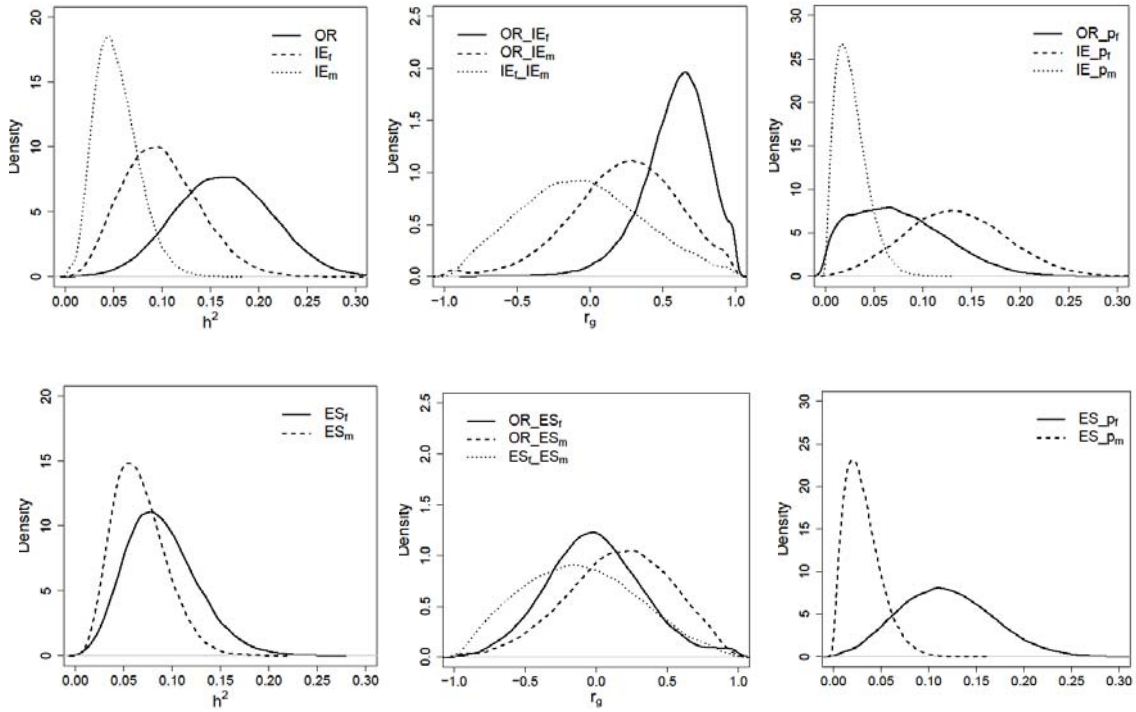

Figure 1: Ratios of variance components for ovulation rate (OR) and female and male contributions to number of implanted embryos (IE_f and IE_m, respectively) and embryo survival (ES_f and ES_m, respectively): h^2: heritability; r_g: genetic correlation; p_f: female permanent environmental effects and p_m: male permanent environmental effects.

As expected, the proportion of variation due to the male non-additive genetic plus permanent environmental effects was almost negligible for IE (0.026 [0.001, 0.058]) and slightly greater for ES (0.031 [0.002, 0.067]), being the repeatability for male contribution to these traits around 8 % and 10% respectively. However, the PM [HPD95%] of the rate of the variation due to the female genetic non-additive plus permanent environmental effects for IE and ES were estimated to be 0.13 [0.03, 0.23] and 0.12 [0.03, 0.21], respectively, being the repeatability of the female contribution to these traits around 23 %. The posterior mean of the correlation between permanent environmental effects due to the female for

the different traits were very imprecise, and it is not possible to draw reliable conclusion either. Finally, the residual correlation between the OR and IE was positive and moderate (PM: 0.40, [HPD95%]: [0.32, 0.48]) whereas it was low and negative for OR and ES: -0.12 [-0.21, -0.02].

CONCLUSIONS

This study shows the possible existence of genetic determinism of male contribution to prolificacy at early stages of gestation, which was measured as the number of implanted embryos and embryo survival after natural mating. The heritability for these traits is small but greater than the heritability of male contribution to litter size at parity. However, response to selection to improve male contribution to reproductive performance after natural mating would be still probably low. Further research is needed in order to determine whether there might be an interaction between male genotype and mating conditions (natural mating or AI, sperm dosage, duration of dose storage, etc) such that it would be possible to find the conditions that give the maximum genetic progress in a breeding program for male fertility and prolificacy and, in turn, an improvement of semen characteristics.

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