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GENETIC PARAMETERS OF OVULATION RATE, EMBRYO AND FETAL SURVIVAL IN RABBITS

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ABSTRACT

An elliptic selection experiment on ovulation rate and prenatal survival was performed. 119 does (group G1) were laparoscopized at day 12 of gestation, and ovulation rate was recorded. 44 G1 does were selected on ovulation rate and prenatal survival by a quadratic index. An average of 2.73 daughters per doe were taken to constitute group 2 (G2). 54 contemporary related females of the same line, laparoscopized for other experiments, were included in the analysis. The estimates of the genetic parameters were obtained by residual maximum likelihood (REML). Heritabilities of ovulation rate (TOR), prenatal survival (PS) and total live embryos at 12 days of gestation (TLE) were 0.21±0.11 and 0.23±0.10 and 0.26±0.10 respectively. Genetic correlations were -0.14±.35 between TOR and PS, 0.36±0.31 between TOR and litter size at birth (LS), and 0.87±0.08 between PS and LS. Left and right sides were analysed separately.

INTRODUCTION

Direct selection for litter size in rabbits has had little sucess (Rochambeau, 1988). In pigs, in which the situation is the same (Haley, Avalos and Smith, 1988), it has been suggested to increase litter size by selection on its two main components, ovulation rate and prenatal survival (Johnson, Zimmerman and Kittock, 1984). Selection only on ovulation rate has been effective but no correlated response in litter size at birth has been found due to a correlated increment in embryo and/or fetal mortality. (Johnson et al., 1984).

The aim of this paper is to estimate the phenotypic and genetic parameters of ovulation rate and prenatal survival necessary for a selection index.

MATERIAL AND METHODS

Experimental design

An elliptic selection experiment on ovulation rate and prenatal survival was performed. This technique optimizes the use of the information to estimate genetic correlations (Cameron and Thompson, 1986). 119 does (group G1) were laparoscopized at day 12 of gestation, and ovulation rate was recorded. 44 G1 does were selected on ovulation rate and prenatal survival by a quadratic index , $I = X' P^{-1} X$, in which X is the vector of data and P the phenotypic variance-covariance matrix of these traits. An average of 2.73 daughters per doe were taken to constitute group 2 (G2). The selection pressure used was calculated to optimize the design (Blasco et al., 1990).
As there were 54 contemporary females of the same line, laparoscopized for other experiments, and the relationship matrix was available, their data were included in the analysis. Therefore, a total of 293 does were laparoscopized, and a total of 399 animals were included in the relationship matrix.

Animals

All the animals came from a synthetic line (line V) formed by mating crossbred males and crossbred females of different origins. Line V has been selected 8 generations on litter size at weaning.

Laparoscopy was performed on pregnant does in their second gestation, 12 days after mating. Some of these does were still lactating. Number of corpora lutea and live and regressed embryos were recorded. Live and regressed embryos can be distinguished by the different size of the swellings, the size of the swellings of regressed embryos being much smaller and having a reduced vascular supply. The laparoscopy technique has been developed by F. García and is described by Santacreu et al. (1990). This technique allows the number of corpora lutea and implanted embryos to be counted accurately without damaging litter size (Santacreu et al., 1990).

Traits analyzed

ROR: right ovulation rate -estimated as number of corpora lutea on the right ovary counted by laparoscopy.
LOR: left ovulation rate. Estimated in the same way as ROR.
TOR: total ovulation rate = ROR + TOR.
RLE: number of live embryos in the right uterine horn at 12 days -estimated as the number of normal uterine swellings in the right horn by laparoscopy-.
LLE: number of live embryos in the left uterine horn. Estimated in the same way as RLE.
TLE: total live embryos = RLE + LLE.
ES : total embryo survival -estimated as TLE/TOR-.
LS : number of total young rabbits at birth.
PS : prenatal survival -estimated as LS/TOR-.
FS : foetal survival from 12 days of gestation -estimated as LS/TLE-.

Statistical Analysis

The estimates of the genetic parameters were obtained by applying residual maximum likelihood (REML) on the following model:

$y = G + L + c + a + e$

Where G is the group effect with two levels, G1 and G2 (fixed).
L is the lactation effect, with two levels: L1 when the doe has suckling young rabbits at mating and L2 otherwise (fixed).
c is the common litter effect of the does born in the same parity (random).
a is the genetic effect of the doe (random).
e is the residual effect (random).

The computing cost of REML analysis is very high, and several algorithms and algebraic techniques have been proposed to reduce this cost. Thompson (1976) proposed a canonical transformation to analyze multivariate REML by performing several univariate analyses on transformed independent variates. This transformation only can be done when the model has two random factors -one factor and the residual- and when all the traits have the same design matrix - which is the case of this experiment.

The process of analysis had the following steps:

1. Univariate analysis were performed, σ^2_a, σ^2_c and σ^2_e were estimated and

$$h^2=\frac{\sigma^2_a}{\sigma^2_y} \quad ; \quad c^2=\frac{\sigma^2_c}{\sigma^2_y}$$

calculated. A derivative free algorithm (Smith and Graser, 1986), computationally efficient, was used. It is difficult to find accurate estimates of the standard errors when this algorithm is used. A DFREML package (Meyer 1988) was used.

2. When $c^2=0$, the canonical transformation was applied and several univariate analyses were performed on a model without common litter effects to estimate the genetic correlations and the heritabilities. The EM algorithm (Dempster et al. 1977), which gives better estimates of the standard errors, was used. The REML-PK package (Meyer 1987) was used.

When many traits are simultaneously analysed, and the data base is not very large, there is a high probability of finding a genetic variance-covariance non-positive definite matrix. Therefore, several analyses with few variables were performed.

REML has been proved to be a useful technique to estimate genetic parameters free of the selection bias (Gianola et al. 1989). Ovulation rate and prenatal survival were included in all the analyses to avoid the bias of selection.

RESULTS

The means, standard deviations, coefficients of variation, and group and lactation effects are shown in table 1. The mean of ovulation rate found in this experiment is higher than the means reported before (Adams, 1960; Hulot and Matheron, 1979; Bolet et al.1990). Embryo and fetal survival are not very different from those found by Adams (1960), Torres (1982) and Molina (1987) - although Plá (1984) obtained a lower value of embryo survival-. Right and left sides present the same values, as it would be expected, but Adams (1960) gives a higher ovulation rate for the right ovary.

TABLE 1. Means (m), standard error of the mean (se), deviations (σ), coefficient of variation (CV) and group (G1-G2) and lactation (L1-L2) effects.

	m	se	σ	CV	G1-G2	L1-L2
TOR	15.16	0.13	2.21	0.15	-0.32	0.12
TLE	12.78	0.15	2.59	0.20	-0.61*	0.25
LS	10.26	0.15	2.59	0.25	+0.19	0.50
PS	0.68	0.01	0.17	0.25	0.02	0.03
ES	0.85	0.01	0.15	0.18	-0.02	0.01
FS	0.81	0.01	0.15	0.19	0.04*	0.02
ROR	7.71	0.13	2.30	0.30	-0.52*	0.14
LOR	7.45	0.14	2.35	0.32	0.20	-0.02
RLE	6.40	0.13	2.15	0.34	-0.61*	0.27
LLE	6.37	0.13	2.25	0.35	-0.003	-0.03

TOR: total ovulation rate. TLE: total number of embryos. LS: litter size at birth. PS : prenatal survival. ES: total embryo survival. FS: foetal survival. ROR: right ovulation rate. LOR: left ovulation rate. RLE: number of live embryos in the right uterine horn. LLE: number of live embryos in the left uterine horn.

The group effect found in some traits can be explained by the seasonal period in which the does were mated -García et al. (1983) found seasonal differences in pre- and postimplantation mortalities-. It has been suggested that a lactation effect could be expected on ovulation rate and prenatal survival (García and Pérez, 1989), however this effect has not been found in our experiment.

The h^2 and c^2 of the univariate analyses are shown in table 2. Comparing the

results of table 2 and tables 3 and 4 it seems that the bias due to selection is rather irrelevant. The common litter effects were small in all the cases, therefore multivariate analyses were performed on a model without common litter effects. There is a surprising difference between the right and left ovaries which we have not been able to explain. Both ovaries have a similar heritability but the right ovary presents some common litter effects. There are some results in pigs showing a different genetic determination of left and right ovaries (Haley and Lee 1992; Kelly et al., 1985) and in mice (Clutter et al., 1990), but it is difficult to believe that there are differences in c^2. When c^2 is ignored in the model, h^2 of the right ovary is higher than h^2 of the left ovary.

We have not found estimates of genetic parameters for componentes of litter size in rabbits in the literature, thus we are obliged to compare our results with other species estimates. Our h^2 of ovulation rate (tables 3 and 4) is lower than the average value of several experiments reviewed by Bidanel (1989), 0.32, although these estimates varied from 0.10 to 0.59. The h^2 of prenatal survival is moderately high, and different from the null value obtained by Haley and Lee (1992). The h^2 of litter size at birth is higher than the h^2 of number of rabbits born alive -highly related to total born- estimated analyzing a large set of data of the same line (0.07, Baselga et al. 1991), probably due to the concentration of all the data in two periods and one parity and/or to the high standard error of this sample.

The heritability of total live embryos has been estimated in pigs near the middle of the gestation -50 days- by Neal et al.(1989), giving a value of 0.08 ± 0.10, lower than the value we have found.

TABLE 2. Heritabilities (h^2) and common litter effects(c^2).

	h^2	c^2		h^2	c^2
TOR	0.23	-0.01	ROR	0.12	0.14
TLE	0.18	0.11	LOR	0.11	0.00
LS	0.27	0.03	RLE	0.14	0.05
PS	0.21	0.01	LLE	0.13	0.06
ES	0.08	0.10			
FS	0.18	-0.01			

TOR: total ovulation rate. TLE: total number of embryos. LS: litter size at birth. PS : prenatal survival. ES: total embryo survival. FS: foetal survival. ROR: right ovulation rate. LOR: left ovulation rate. RLE: number of live embryos in the right uterine horn. LLE: number of live embryos in the left uterine horn.

The main correlations are shown in table 3. Genetic and phenotypic correlations do not seem to be very different in our case. The most remarkable results are the low correlations between ovulation rate and either litter size and prenatal survival, and the high correlations between prenatal survival and litter size. In pigs, the estimates of the genetic correlation between ovulation rate and litter size give values near zero (Young et al., 1978; Cunningham et al., 1979; Neal and Johnson, 1986) with the exception of Haley and Lee (1992), 0.98 ± 0.01. We have not found estimates of genetic correlations between prenatal survival and either ovulation rate and litter size in pigs. In mice Clutter et al (1990) give estimates of 0.06 and 0.60 between prenatal survival and ovulation rate, and between prenatal survival and litter size respectively (standard errors within a range from 0.06 to 0.66). We have not found estimates of correlations between number of live

embryos and litter size. An estimate of 0.18±0.13 is given by Johnson et al. (1984) in pigs, but due to the high mortality produced by the surgical technique, this result has to be taken with caution.

Genetic and phenotypic correlations of ovulation rate with total live embryos are moderatly high. The only published data in pigs are 0.21±0.42 by Neal et al. (1986) and -0.56±0.24 by the same team using a larger number of data (Neal et al. 1989), and 0.65±0.38 (Bolet et al. 1989).

TABLE 3. Heritabilities (diagonal), genetic correlations (below the diagonal) and phenotypic correlations (above the diagonal) of the main traits. Standard errors between brackets.

	TOR	PS	LS	TLE
TOR	0.21 (0.11)	-0.30 (0.05)	0.25 (0.06)	0.49 (0.04)
PS	-0.14 (0.35)	0.23 (0.10)	0.84 (0.02)	0.39 (0.05)
LS	0.36 (0.31)	0.87 (0.08)	0.29 (0.12)	0.68 (0.03)
TLE	0.66 (0.22)	0.56 (0.26)	0.87 (0.11)	0.26 (0.10)

TOR: total ovulation rate. PS : prenatal survival. LS: litter size at birth. TLE: total live embryos.

Table 4 shows the relationships between the right and left ovaries and between ovulation rate and embryo survival of both sides separately. As c^2 was not considered in the analysis the results of both sides are not the same. Correlations between ovulation rates are both genetic and phenotypic negative, however, Clutter at al. (1990) found positive correlations in mice (0.72 and 0.70 respectively), and Haley and Lee (1992) gave a positive genetic correlation (0.94, without standard error) and a negative phenotypic correlation (-0.52).
It is possible to find a negative phenotypic correlation between the ovulation rate of both ovaries, but it is more difficult to explain a negative genetic correlation.

Table 4 also shows the relationships between embryo and fetal survival. The phenotypic correlation is close to zero, and the estimate of the genetic correlation is positive, but the standard error is very high and this result should be taken with caution.

DISCUSSION

Correlations near -0.8 were used for the experimental design, but the low correlations found between ovulation rate and prenatal survival affected the expected standard errors -which should have been lower.

Despite having a high coefficient of variation and a heritability different from zero, litter size has not been significantly improved (Rochambeau 1988). Also, no improvement in litter size has been found when ovulation rate was selected in pigs (Johnson et al., 1984) and mice (Bradford, 1969).

The small correlations between ovulation rate and either litter size and prenatal survival, the high correlations between prenatal survival and litter size and the moderatly high heritability of prenatal survival suggest that prenatal survival could be used as a trait for indirect selection on litter size, and gives relevance to the experiments about uterine capacity that are being currently performed (Argente et al. 1992; Bolet 1992, personal communication).

TABLE 4. Heritabilities (diagonal), genetic correlations (below the diagonal) and phenotypic correlations (above the diagonal) Standard errors between brackets.

	TOR	PS	ES	FS		TOR	PS	LOR	ROR
TOR	0.21 (0.10)	-0.29 (0.05)	-0.22 (0.05)	-0.19 (0.06)	TOR	0.20 (0.11)	-0.30 (0.06)	0.50 (0.05)	0.44 (0.05)
PS	-0.07 (0.36)	0.17 (0.09)	0.68 (0.03)	0.70 (0.03)	PS	-0.17 (0.37)	0.22 (0.11)	-0.11 (0.06)	-0.17 (0.06)
ES	0.21 (0.52)	0.81 (0.25)	0.09 (0.08)	-0.03 (0.06)	LOR	0.32 (0.43)	-0.16 (0.48)	0.11 (0.09)	-0.55 (0.04)
FS	-0.29 (0.38)	0.91 (0.13)	0.49 (0.58)	0.17 (0.10)	ROR	0.71 (0.25)	-0.04 (0.38)	-0.44 (0.38)	0.21 (0.11)

	TOR	PS	LOR	LLE		TOR	PS	ROR	RLE
TOR	0.19 (0.11)	-0.30 (0.06)	0.50 (0.05)	0.32 (0.05)	TOR	0.19 (0.10)	-0.30 (0.05)	0.44 (0.04)	0.25 (0.04)
PS	-0.17 (0.37)	0.22 (0.11)	-0.11 (0.06)	0.22 (0.06)	PS	-0.14 (0.37)	0.22 (0.11)	-0.17 (0.05)	0.25 (0.04)
LOR	0.31 (0.42)	-0.17 (0.46)	0.12 (0.09)	0.82 (0.02)	ROR	0.70 (0.26)	-0.01 (0.38)	0.18 (0.09)	0.73 (0.02)
LLE	0.39 (0.37)	0.19 (0.39)	0.90 (0.13)	0.17 (0.10)	RLE	0.45 (0.33)	0.68 (0.20)	0.73 (0.18)	0.11 (0.05)

TOR: total ovulation rate. PS : prenatal survival. ES: total embryo survival. FS: foetal survival. LOR: left ovulation rate. ROR: right ovulation rate. RLE: number of live embryos in the right uterine horn. LLE: number of live embryos in the left uterine horn.

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