DIVERGENT SELECTION FOR UTERINE EFFICIENCY IN UNILATERALLY OVARIECTOMIZED RABBITS. I. PHENOTYPIC AND GENETIC PARAMETERS.

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SUMMARY

Two experiments of divergent selection for uterine efficiency in rabbits were performed. Rabbit does were unilaterally ovariectomized and a laparoscopy was made at mid-gestation to observe the number of corpora lutea and implanted embryos in the functional genital tract. Selection was based on the number of fetuses which died between implantation and birth in the first experiment, and on litter size in the second one, both using BLUP on an animal model. This paper presents the average values of observed traits and their heritability. Results show that an effective overcrowding of one uterine horn was obtained at implantation. The additive genetic variability of embryonic survival seems to be greater than that of fetal survival. Some differences in heritabilities between intact and unilaterally ovariectomized females tend to appear.

INTRODUCTION

Selection on uterine efficiency might become an indirect way of improving litter size. Christenson et al (1987) suggested use of unilateral ovariectomy and hysterectomy in pigs to measure uterine capacity. The latter was defined as the maximum number of fetuses the dam can support at birth when the number of ova shed is not a limiting factor. Uterine capacity would then depend on two main traits : the number of implantation sites and fetal survival (or the number of fetuses the uterus can support to term). As these traits are not necessarily related to the length or volume of the uterus, we prefer to use the expression "uterine efficiency" instead of "uterine capacity".

In rabbits, unlike pigs, transuterine migration is almost never found ; thus unilateral ovariectomy and consequent ovarian hyperactivity (Fleming et al, 1984; Mariana and Dervin, 1992) results in the corresponding horn facing twice the mean normal number of embryos, without hysterectomy. It is possible to observe the number of corpora lutea and implantation sites by laparoscopy in rabbits, without affecting litter size (Santacreu et al, 1990).

The objective of this paper is to analyse the results of two divergent selection experiments on uterine efficiency, measured in one case in terms of litter size, and in the other in terms of the number of fetuses which died between implantation and birth, both in unilaterally ovariectomized (ULO) females.

MATERIAL AND METHODS

Two divergent selection experiments were performed. In both cases the divergent lines were initiated by selecting daughters and sons from the best and worse females of the base generation (G0). Technical procedures for ovariectomies and laparoscopies (Garcia-Ximenez, 1992) were the same in both experiments.

1. Experiment 1.

All rabbits came from a synthetic population bred at the INRA experimental farm in Auzeville. Each divergent line had 120 females and 6 males per generation. Females were artificially inseminated, the ovulation being induced with 0.2ml of GnRH (Receptal, Distrivet).

From the base (G0) to the third (G2) generation, the first insemination occured when the females were 18 weeks old. Ovulation was again induced after the weaning and the right ovary was removed. The number of corpora lutea of both ovaries were then recorded. One month later, the does were again inseminated. A laparoscopy was performed around the 10th day of this second gestation, and the number of corpora lutea and implanted embryos in the functional genital tract were recorded. At weaning, a third ovulation was induced and the number of corpora lutea was immediately counted during autopsy. At the 4th generation (G3), only half of the females were unilaterally ovariectomized (this time before puberty). A laparoscopy was then performed in half of the females of both types during the first gestation, and in all of them in the second gestation. At the 5th generation (G4), all of the females were intact, and only 30 to 50% of them were laparoscopized in each gestation.

Selection was performed on the number of fetuses which died between implantation and birth during the 2nd gestation, trying to decrease it (H line) or increase it (L line). BLUP was performed on an animal model with generation and sire fixed effects, for the 2 divergent lines together, by using the PEST program (Groeneveld et al, 1990).

2. Experiment 2.

The animals were derived from a synthetic line selected on litter size, which was founded by mating crossbred males and females of different genetic origins. They were bred at the experimental farm of the Universidad Politécnica de Valencia. The left ovary was removed before puberty, when the females were 14 to 16 weeks old. Each divergent line had 40 females and 12 males per generation. The females were first mated when they were around 18 weeks old and thereafter 10 days after littering. A laparoscopy was performed on all does during their second gestation, 12 days after mating, and the number of corpora lutea and implanted embryos were recorded. The 2 divergent lines were selected over 4 generations to increase (H line) or decrease (L line) litter size by using a BLUP procedure on a repeatability animal model, with fixed effects generation and parity.

3. Statistical analysis

Data from the 2 experiments were analyzed separately. The traits analyzed were the total number of corpora lutea (CL), the total number of implanted embryos (IE), the litter size at birth (LS), the number of fetuses which died after implantation (ND=IE-LS), and the embryonic (ES=IE/CL), fetal (FS=LS/IE), and prenatal (PS=LS/CL) survival rates. Least square means were calculated from a model with generation and line within generation fixed effects. When data from several parities were analyzed, parity was included as a fixed effect, and also the number of ovaries in the 1st experiment. Heritabilities of the characters were calculated with univariate REML analyses, on an animal model with generation, and if required parity and number of ovaries, fixed effects. CL and LS heritabilities were also estimated using a repeatability animal model. In experiment 1, data from ULO and intact females were also analysed separately. Groeneveld's (Groeneveld, 1993) and Meyer's (Meyer, 1987) computer programmes were used.

RESULTS

1. Means and phenotypic variability

Table 1 shows the mean values of the traits and their standard deviation with 1 ovary in both experiments, and also before ovariectomy in the 1st one, for gestations in which CL, IE and LS were recorded. With one ovary, rabbits from experiment 2 had more corpora lutea and implanted embryos than those from experiment 1, but the same embryonic survival. The litter size was also higher, in spite of a lower fetal survival.. In experiment 1, there were no significant differences between ULO and intact females, except for litter size, which was reduced by 11% ($P<0.01$). Coefficients of variation tended to be higher in experiment 1 for numbers of ova, embryos or young, but were very similar in both experiments for survival rates. In experiment 1, the variability of traits or survival rates were not affected by ovariectomy.

2. Genetic variability

a. Data from unilaterally ovariectomized does :

Heritabilities in experiment 2 tended to be greater than those in experiment 1. However, their standard error was generally higher, because of a lower amount of data. In both experiments, the heritability of the number of ova shed was similar (0.23 to 0.30) and significantly different from zero. The heritability of the number of implanted embryos and litter size was not different from zero in experiment 1, whereas it was higher in experiment

2. In both experiments, heritabilities of fetal survival and of the number of dead fetuses were not significantly different from zero, whereas the heritability of embryonic survival (at least in experiment 1) and prenatal survival (0.11 to 0.18) tended to be positive.

When a random repeatability effect was considered in the model for the number of corpora lutea and litter size, the value of heritability was similar to that shown in table 1, and the repeatability effect was low and not significantly different from 0 in both experiments. In experiment 2, the heritability of LS became significantly different from zero.

b. Comparison between data from intact and ULO females (experiment 1) :

The heritability of the number of ova shed was very similar, whereas the heritability of the number of implanted embryos and litter size was significantly positive only in intact females. The values of heritabilities of embryonic and prenatal survival were in the same range, whereas the heritability of fetal survival and of the number of dead fetuses was only significantly different from zero in intact females.

Table 1. Least square means and standard deviation (s) of litter size (LS), number of corpora lutea (CL), number of implanted embryos (IE), embryo, fetal and prenatal survival rates (ES, FS, PS) and number of dead fetuses (ND). (n=number of data)

	Experiment 1				Experiment 2	
	Intact females n=371		Unilaterally ovariectomized n=605		Unilaterally ovariectomized n=291	
	mean	s	mean	s	mean	s
LS	7.2	2.8	6.4	2.2	7.7	2.4
CL	10.4	2.9	10.0	2.1	14.4	2.1
IE	8.4	3.3	7.8	2.5	11.0	2.8
ES	0.80	0.22	0.79	0.22	0.78	0.19
FS	0.89	0.19	0.85	0.19	0.71	0.19
PS	0.70	0.22	0.66	0.23	0.55	0.18
ND	1.1	1.7	1.4	1.7	3.3	2.4

Table 2. Heritability (h^2) (with standard error σ) of litter size (LS), number of corpora lutea (CL), number of implanted embryos (IE), embryo, fetal and prenatal survival rates (ES, FS, PS) and number of dead fetuses (ND). (n=number of data)

	Experiment 1						Experiment 2		
	Intact females			Unilaterally ovariectomized females			Unilaterally ovariectomized females (2nd parity)		
	n	h^2	σ	n	h^2	σ	n	h^2	σ
LS	1630	0.11	0.02	722	0.05	0.03	291	0.20	0.12
CL	1174	0.24	0.04	1226	0.23	0.03	291	0.30	0.11
IE	464	0.18	0.04	707	0		291	0.28	0.10
ES	458	0.07	0.04	654	0.09	0.03	291	0.10	0.08
FS	376	0.18	0.02	651	0		291	0.15	0.13
PS	375	0.08	0.06	607	0.11	0.03	291	0.18	0.09
ND	376	0.27	0.10	651	0		291	0.26	0.16

DISCUSSION

According to data from experiment 1, the ovarian activity was almost fully restored after unilateral ovariectomy, but the litter size was significantly affected, as was the case in pigs (Christenson et al, 1987), in mice (Clutter et al, 1990 ; Kirby and Nielsen, 1993), and in rabbits from experiment 2 (Argente et al, 1992). This reduction of prenatal survival in experiment 1 was due essentially to a decrease of fetal survival, by 5% (P<0.07), without any reduction of embryonic survival. So, the experimental procedure resulted in an effective double crowding at implantation in one uterine horn. However, Argente et al (1992) observed that unilateral ovariectomy significantly affected ES, but not FS. We may suppose that this difference is due to the strains used in the 2 experiments. However the point remains to be verified.

The number of ova shed (CL) was the trait for which heritability was the highest in both experiments (0.25-0.30). It is similar to values observed in intact females, in rabbits and pigs (Blasco et al, 1994) and in mice (Clutter et al, 1990). This is confirmed by the absence of difference of heritability for CL in experiment 1 between ULO and intact does.

The average value of heritabilities observed in experiment 2 are in good agreement with results obtained in intact females from the same base population (Blasco et al, 1993), but because of their standard deviation, this result will have to be confirmed with more data. The heritability of prenatal survival was positive in both experiments (0.10-0.18), which is in agreement with results obtained in pigs (Blasco et al, 1994) and mice (Clutter et al, 1990), in intact females. In both experiments, it seems that the additive genetic variability of fetal survival is low, whereas that of embryonic survival tends to be higher, at least in experiment 1, which does not match with the result of Blasco et al (1993) in intact females. This means that the genetic variability could be greater for embryonic than for fetal survival. However, it should be noted that, in intact females from experiment 1, the additive genetic variability of fetal survival was significantly greater, which could mean that the genetic determinism of this trait is different in the two situations. This will have to be verified with the genetic correlations between characters of intact and operated females.

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