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SELECTION FOR UTERINE CAPACITY. II RESPONSE TO SELECTION ESTIMATED WITH A CRYOPRESERVED CONTROL POPULATION.

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ABSTRACT

Intact females of the 11th generation of selection from two lines selected divergently for uterine capacity (UC+ and UC-) and from a cryopreserved control population (C) were used. Uterine capacity was estimated as litter size in unilaterally ovariectomized females. The traits recorded for up to 5 parities for female were: Litter size (LS), number of born alive, number alive at first week of age and number of weaned. A laparoscopy was performed in all females at the 12th day of their second parity and the ovulation rate (OR) and number of implanted embryos (IE) were recorded. Embryo survival (ES=IE/OR), fetal survival (FS=LS/IE) and prenatal survival (PS=LS/OR) were computed. The response to divergent selection was not symmetrical, the line UC- showed a lower LS than the control line, the difference being 2.1 young rabbits, but the difference between UC+ and C was 0.57 young rabbits. The lower LS in UC- line seems to be due to a lower OR (13.44 versus 14.85) and a lower ES before implantation. There were no differences between both lines for FS. Differences in litter size between divergent lines (UC+ y UC-) seemed to be associated with a higher number of implanted embryos (IE) and embryo survival (ES). The lack of symmetry in the response can be explained by the presence of a major gene affecting both UC and ES.

INTRODUCTION

Response to selection can be estimated by separating genetic and environmental effects analyzing the data with BLUP/REML techniques on a mixed model, or using Bayesian techniques. These procedures do not need the use of control populations, but their results have an strong dependence on the reliability of the assumptions. For example, SORENSEN and JOHANSON (1992) shown that the estimated response to selection using BLUP, depend much more on the estimated variance components used than on the true components. Control populations are particularly useful in divergent selection experiments because they allow the detection of asymmetric responses. A main problem of the use of control populations is the need of employing experimental facilities that could be used by the lines that are selected. Another problem is that genetic drift can move control populations forward or downwards the average of the unselected trait. Although they have been rarely used in selection experiments, frozen control populations have the advantages of a better use of the experimental facilities and a reduction of the genetic drift. Besides, frozen control populations avoid the unadvertised selection on related traits that often occurs, and also reduces the effect of Natural selection. In a companion paper (BLASCO et al., 2000) estimated the responses of a divergent selection experiment on uterine capacity by using least squares, BLUP/REML and Bayesian techniques. We will estimate now these responses to selection by using a frozen control population.

MATERIAL AND METHODS

Animals

Intact females of the 11th generation of selection from two lines selected divergently for uterine capacity (Blasco et al., 2000) and from a cryopreserved control population (García *et al*., 1998) were used. Uterine capacity was estimated as litter size in unilaterally ovariectomized females. In order to avoid some effect of cryopreservation in the reproductive traits (Cifre *et al.*, 1999), the control population was created with offspring of the cryopreserved embryos. Data from 702 parities corresponding to 211 intact females were used: 78 does from the line selected for high uterine capacity (UC+), 64 females from the low uterine capacity line (UC-), and 69 females from the control line (C). All females used in this experiment had both uterine horns functional.

Traits

The traits recorded for all parities (up to 5 parities for female) were: Litter size (LS), number of born alive (NBA), number alive at first week of age (N1wk) and number of weaned (NW). A laparoscopy was performed in all females at the 12th day of their second parity and ovulation rate (OR) and number of implanted embryos (IE) were recorded. Litter size at the second parity (LS2), embryo survival (ES=IE/OR), foetal survival (FS=LS2/IE) and prenatal survival (PS=LS2/OR) were also analysed.

Statistical Analyses

LS, NBA, N1wk and NW were analysed by least squares using a model with the fixed effects of line (UC+, UC-, control), season (spring, summer, autumn and winter), farm (with two levels corresponding to the two farms in which the animals were reared) and lactation-parity with 9 levels (nulliparous does, does of second parity mated at 10, 17, 24 and 31 days after their first birth, and does with more than two parities mated at 10,17,24, and 31 days after their last birth). Traits of the second parity were studied using the same model, but the three levels for the season (summer, autumn and winter). The procedure GLM of the SAS statistical package was used (SAS, 1997).

RESULTS AND DISUCSSION

Table 1 shows the contrasts between lines for litter size traits. A high divergence between UC+ and UC- is observed, but it seems to be originated mainly by high response in the UC- line and a much lower response in the line UC+. Response to selection was thus not symmetrical. This contradicts the results found in the companion paper (Blasco et al., 2000), in which symmetrical responses were estimated using Bayesian techniques applied to all data of the selection process. The reasons for these contradictory results are not clear, and they can be due to the high standard errors that usually appear when comparing data of selected and control populations. When response to selection is estimated by BLUP/REML or Bayesian techniques, the amount of information used is much higher and consequently the precision is also higher than when response is estimated comparing selected and control populations in the last generation of selection. Moreover, our standard errors are slightly underestimated, since they come from a model in which the relationships between individuals were not taken into account. However there is an alternative explanation for these differences found in the estimation of the response. As Argente et al. (2000, a) show in another paper presented in this Congress, it is likely that a major gene affecting uterine capacity is segregating in our population. Our UC lines were originated from a population previously selected on litter size. Argente et al. (2000, b) have shown that litter size and uterine capacity are highly genetically correlated, therefore we can expect a high frequency of the favorable allele for uterine capacity in our population. The effect of the favorable allele will be imperceptible in the line selected for UC, but the unfavorable allele will be quickly selected in the low line. In mice, Falconer (1960) found that selection to reduce litter size lead quickly to a higher mortality and suggest that is due to an increase of gene frequency with deleterious effects, which might be an alternative explanation to the high response found in the low line, but this would not explain the large divergence found in the first generation of selection (BLASCO et al., 2000).

In mice, selection to increase uterine capacity has been also effective, the difference being of 1.67 pups between a control and selected population in the 21th generation (Kirby and Nielsen, 1993). In the 13th generation, the response estimated was of 0.79 pups (Gion *et al*., 1990), similar to the result obtained in this experiment in the 11th generation (0.57 young rabbits, table 1). However selection for high uterine capacity was not more efficient than selection for litter size (Kirby and Nielsen, 1993). A contemporaneous comparison was made between a line selected for number of young rabbits at weaning and the same control line used in this experiment (García et al., 2000). The response found was of 0.61 for number of total born (LS), similar to the response found in the high line.

Table 1. Contrasts between selected and control lines, with standard errors (between brackets) for litter size (LS), number of born alive (NBA), number of alive at first week (N1wk) and number of weaned (NW)

	C - (UC+)	C - (UC-)	(UC+) - (UC-)	C
LS	-0.57 *	2.06 *	2.63 *	10.11
	(0.27)	(0.29)	(0.27)	(0.24)
NBA	-0.18	2.20 *	2.38 *	9.66
	(0.30)	(0.32)	(0.30)	(0.26)
N1wk	-0.01	1.86 *	1.87 *	8.79
	(0.28)	(0.29)	(0.28)	(0.25)
NW	-0.07	1.92 *	1.99	8.26
	(0.27)	(0.29)	(0.27)	(0.24)

UC+: line selected for high uterine capacity. UC-: line selected for low uterine capacity. C: control line.

Although the high divergence between UC+ and UC- lines was maintained after birth, (table 1), an apparent reduction in litter size after birth appears in the UC+ line, but the large standard errors do not allow to draw clear conclusions. The contemporaneous line selected for litter size at weaning showed a response for NW of 0.53 young rabbits (García et al., 2000).

The lower litter size in UC- line respect to C line seems to be due to both a lower ovulation rate (OR) and higher embryo mortality before implantation (table 2), instead of a competence for the nutrients and space after implantation, since there were not differences between lines for foetal survival. In the selection experiment for uterine capacity in mice, response in litter size in intact females was due to a small increase in both components of litter size, ovulation rate (0.81 ovules) and prenatal survival (5%). In the selection experiments for litter size, response was mainly due to an increase in ovulation rate, not only in rabbits García *et al*. (2000), but also in pigs and mice (see reviews by Blasco *et al*., 1993, 1995). Here, differences in litter size between divergent lines (UC+ y UC-) seemed to be associated to a higher number of implanted embryos and a higher embryo survival. Differences in number of implanted embryos can be due to differences in hormones and proteins present in the uterine secretion. An experiment comparing concentrations of estradiol, progesterone, and uteroglobin between UC lines is now being carried out.

Table 2. Contrasts between selected and control lines and standard errors (between brackets) of ovulation rate (OR), number of implanted embryos (IE), litter size (LS2), embryo survival (ES), foetal survival (FS) and prenatal survival (PS).

	C - (UC+)	C - (UC-)	(UC+) - (UC-)	C
OR	0.86 *	1.41 *	0.55	14.86
	(0.42)	(0.46)	(0.44)	(0.34)
IE	0.26	2.37 *	2.10 *	12.63
	(0.49)	(0.53)	(0.51)	(0.39)
LS2	-0.44	2.34 *	2.78 *	9.76
	(0.53)	(0.58)	(0.55)	(0.42)
ES	-0.03	0.09 *	0.12 *	0.86
	(0.03)	(0.03)	(0.03)	(0.02)
FS	-0.05	0.05	0.10	0.70
	(0.05)	(0.05)	(0.05)	(0.04)
PS	-0.07	0.09	0.16 *	0.61
	(0.05)	(0.05)	(0.05)	(0.04)

UC+: line selected for high uterine capacity. UC-: line selected for low uterine capacity. C: control line.

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