Proceedings of the

7th World Rabbit Congress

4-7 july **2000** – Valencia Spain

These proceedings were printed as a special issue of WORLD RABBIT SCIENCE, the journal of the World Rabbit Science Association, Volume 8, supplement 1

ISSN reference of this on line version is 2308-1910
(ISSN for all the on-line versions of the proceedings of the successive World Rabbit Congresses)

Blasco A., Ortega J.A., Santacreu M.A.

SELECTION FOR UTERINE CAPACITY. 1 : GENETIC TRENDS AND CORRELATED RESPONSE IN COMPONENTS OF LITTER SIZE.

Volume A, pages 347-352

SELECTION FOR UTERINE CAPACITY. I GENETIC TRENDS AND CORRELATED RESPONSE IN COMPONENTS OF LITTER SIZE.

A. Blasco, J.A. Ortega and M.A. Santacreu

Universidad Politécnica de Valencia. Departamento de Ciencia Animal.
P.O. Box 22012. Valencia 46071. Spain.

ABSTRACT

An experiment of divergent selection for uterine capacity was performed. Rabbit does were unilaterally ovariectomized and a laparoscopy was made at mid gestation to count the number of corpora lutea in order to estimate the ovulation rate (OR) and number of implanted embryos (IE). Uterine capacity was estimated as litter size (UC) in unilaterally ovariectomized females. Selection was performed on UC with all parities. Heritability of UC, OR and IE were 0.09, 0.27 and 0.18. Genetic correlation between UC and OR, and between UC and IE was 0.58 in both cases. Selection on UC was effective, a correlated response was found in IE, and also (to a lower state) in OR. The high difference between high and low lines in the first generation postulates the presence of a major gene controlling UC. Ovulation rate might be an alternative in order to improve litter size with more efficiency than selection for litter size or uterine capacity.
Key Words: Uterine capacity, rabbit, litter size.

INTRODUCTION

Selection for litter size components (ovulation rate and prenatal survival) has not been effective to improve litter size in prolific domestic species (Blasco et al., 1993, 1995, 1998). Selection for increased uterine capacity may provide an indirect way to improve litter size. Only results from one selection experiment in mice have been hitherto published (Kirby and Nielsen, 1993), showing that uterine capacity (UC) was not more effective than selection on litter size. However, although selection on litter size has been effective in several experiments with mice, little success has been found in closed populations of rabbits (Blasco, 1996). In rabbits, Blasco *et al.* (1994) and Bolet *et al.* (1994) have proposed litter size of unilateral ovariectomized does to estimate uterine capacity.

An experiment of divergent selection on uterine capacity was started in 1992. As in rabbits, unlike in pigs or mice, it is possible to observe the number of corpora lutea and implantation sites by laparoscopy without damaging litter size (Santacreu et al., 1990), these traits were also recorded. Some preliminary results of the first four generations of selection have been published by Argente et al. (1997). The objective of this paper is to estimate the genetic and phenotypic parameters of uterine capacity and the genetic responses of a divergent selection experiment on uterine capacity in rabbits. Other papers related to this experiment are presented in this Congress; Argente et al. (2000[a]) examines the genetic correlation between litter size and uterine capacity using intact and ULO females, Santacreu et al. (2000) examines the results of a comparison between both divergent lines and a frozen control population that was thawed to be contemporary of the 10^{th} generation of the divergent lines, Argente et al. (2000[b]) check the presence of a QTL for uterine capacity and Mocé et al. (2000) looks at the evolution of teats number and its relationship with survival.

MATERIAL AND METHODS

Animals

Animals were derived from a synthetic line (V) selected for increased litter size, which was founded by mating crossbred males and females of two commercial hybrids that were commonly used as maternal lines. The founders were chosen at random from line V at generation 12; this is denoted generation zero of the present experiment. At that time, two lines were formed by selecting the offspring of the ovariectomized does with the highest (H) and lowest (L) predicted breeding values. Animals were bred at the experimental farm of the Universidad Politécnica de Valencia. Females were mated 10 days after farrowing. The left ovary of the does was removed before puberty. A laparoscopy was performed in the second parity, 12 days after mating. Surgical techniques have been described with detail by Santacreu et al. (1990) and Argente et al. (1997).

Selection was performed on litter size (i.e. uterine capacity) with data that included records up to parity four in most females, using a BLUP procedure with a repeatability animal model that considered number of generation (an environmental effect, since parities took place within a short interval of time) and parity as fixed effects. Prior values for heritability (h^2) and repeatability (r) were 0.10 and 0.15, respectively. These were estimated using litter size data from the V population, and were used to solve the mixed model equations. Selection was based on the average predicted breeding value of the parents of the candidates, but males were selected within sire families in order to reduce inbreeding. Base generation was composed by 80 females and 24 males. In each divergent selection line there were on average, approximately 40 female and 12 male parents each generation. The total number of records in the H and L lines was 2,344. The experiment included 10 cycles of selection.

Traits

The following traits were analysed: OR: ovulation rate (i.e. number of ova shed) -estimated as number of corpora lutea. IE: number of implanted embryos -estimated as number of implantation sites. UC: uterine capacity (total number of young rabbits born). All the traits were measured in second parity with the exception UC, which was measured in four parities.

Statistical Analyses

Genetic parameters

Phenotypic and genetic parameters were obtained from multivariate REML analyses, using a quasi-Newton procedure, with the VCE computer program (Groeneveld, 1994). Heritability of uterine capacity was estimated with a univariate model. Heritabilities of OR and IE were estimated using bivariate models including litter size, in order to avoid bias due to selection. Relationships between OR and IE could not be estimated in a trivariant analysis because the process did not converge. Uterine capacity was analyzed with a repeatability animal model with a year-season fixed effect of 30 levels, and a fixed effect of lactation-parity with three levels (nulliparous does, lactating does, non-lactating does). The remaining traits were analyzed with an animal model (with no permanent random effects) that included year-season and lactation-parity fixed effects (only with two levels because traits were recorded only in the second parity).

Direct response on uterine capacity

Response to selection for UC was estimated in two ways. The first one was a least squares analysis; with the same model as for genetic parameters, including now a generation effect. The second analysis was based on Bayesian methods using a repeatability animal model. No previous information about effects of season or lactation-parity on uterine capacity was available, therefore an improper uniform prior was used to represent vague previous knowledge about them. Prior knowledge about permanent, additive and residual effects were represented by assuming that these are normally distributed with zero mean and variances $\mathbf{A}\sigma^2_a$, $\mathbf{I}\sigma^2_p$, $\mathbf{I}\sigma^2_e$ respectively. Marginal posterior distributions were obtained using Gibbs sampling techniques. A more detailed description of the Bayesian inference and Gibbs sampling can be found in other paper of this congress, applied to a much more complicated problem (Piles et al., 2000). The results presented here were obtained using a single long chain. Results from other independent chains were very similar and are not reported. Previous analyses led to a choice of chain length equal to 200,000; the burn-in period was set equal to 20,000 iterations. The sampling interval was 60, so that a total of 3,000 samples were kept to estimate features of posterior distributions. Monte Carlo estimates of means and variances of posterior distributions obtained from various chains with these characteristics were practically indistinguishable, and the minor differences could be ascribed to sampling error. The latter was computed using time-series procedures described in Geyer (1992).

Correlated response on litter size components

Correlated response to selection for uterine capacity on ovulation rate and number of implanted embryos was estimated by BLUP on a model with the same fixed effects as before, using the REML estimates obtained. The analyses were performed using the PEST computer program (Groeneveld, 1994). The reason for not performing a complete Bayesian analysis in all variables was the lack of software available, since Monte Carlo Markov Chains techniques for genetic problems have been only recently available.

RESULTS AND DISCUSSION

Table 1 shows the estimates of genetic parameters. Heritability of uterine capacity was deceptively low. Argente et al. (2000[a]) show in other paper presented in this congress that heritability of UC was not higher than heritability of litter size, a result already found in mice (Kirby et al., 1993). Heritabilities of OR and IE were higher, and genetic correlations with UC were considerably high, opening the question of whether selection for OR would be more effective in rabbits that it has been in pigs or mice (see Blasco et al., 1993 for a review). In a previous report with only four generations of selection, the genetic correlation of OR with UC was lower (0.36) and therefore the conclusions about this point were different.

Table 1. Genetic parameters of uterine capacity (UC), ovulation rate (OR) and number of implanted embryos (IE). Heritabilities on the diagonal, genetic correlations below the diagonal. Phenotypic correlations above the diagonal.

	UC	OR	IE
UC	0.09 (0.02)	0.09	0.56
OR	0.58 (0.11)	0.27 (0.06)	0.34
IE	0.58 (0.12)	(*)	0.18 (0.05)

(*) No convergence raised

Figure 1 shows the results of the Bayesian analysis. The averages of the genetic values differ dramatically in the first generation, being maintained in the following ones and slowly progressing afterwards. This leads to the strong suspicion of the existence of a major gene controlling uterine capacity. The main inconvenience against this hypothesis is that the line from which the divergent selection started was previously selected for litter size, thus a gene directly related with litter size should be in a high frequency in the line from which the divergent lines were originated. However, Santacreu et al. (2000) have shown that when comparing both lines with a control population, composed of frozen embryos that were thawed in generation 10, most of the response to selection took place in the low line. This result contradicts the analysis shown in figure 1 and should be taken with caution, but the possibility of the existence of a gene related to uterine capacity deserves further attention. Argente et al. (2000[b]) found some evidences on the existence of a QTL controlling IE, although the evidences in favor of a QTL for UC were inconclusive. Figure 1 shows some of the advantages of Bayesian analyses: confidence intervals (the shortest ones containing the true value with a probability of 95%) have been calculated taking into account the error committed when estimating the heritability of UC, and they are not symmetrical.

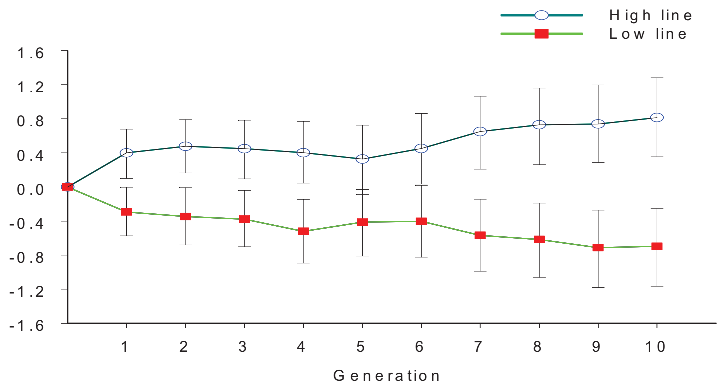

Figure 1. Genetic averages of uterine capacity per generation, with the minimum length 95% confidence intervals.

Figure 2 shows the evolution of the differences between high and low lines. Typically, they look erratic (the amount of information for each difference is much lower than the information used to draw genetic trends), but it should be stressed two important points: first, that the differences between high and low lines were always positive, which leads to suppose that selection was successful, and second that most of the response achieved come from the first generation of selection. With the exception of the results of generation 9, there is a clear link between UC and IE, and a rather vague relationship between UC and OR. When genetic trends are examined (figure 3), these tendencies are confirmed. It seems that UC is related both to OR and IE. Other paper presented in this congress examines the relationships between UC and litter size (Argente et al., 2000[a]) and shows that both traits are almost the same character. Rabbits are peculiar in comparison with other politocous species, since there is no fetal migration between uterine horns. This means that a normal litter size value can come preferentially from one of the uterine horns. Augmenting OR, we could probably provide both uterine horns with ova enough to allow the to express their uterine capacity. There are several indications in favor of ovulation rate

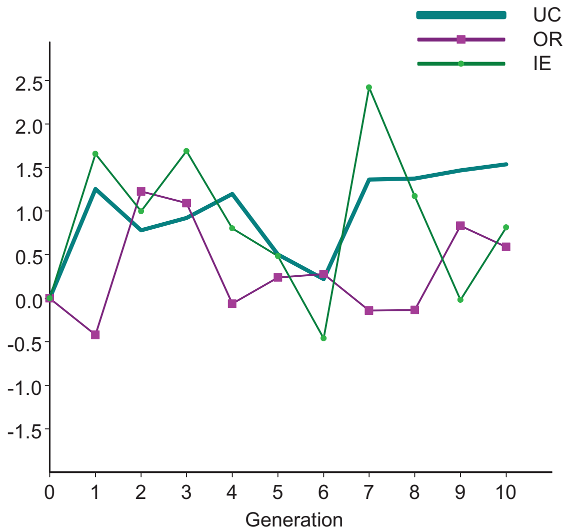

Figure 2. Differences in uterine capacity (UC), ovulation rate (OR), and number of implanted embryos (IE) per generation between high and low lines.

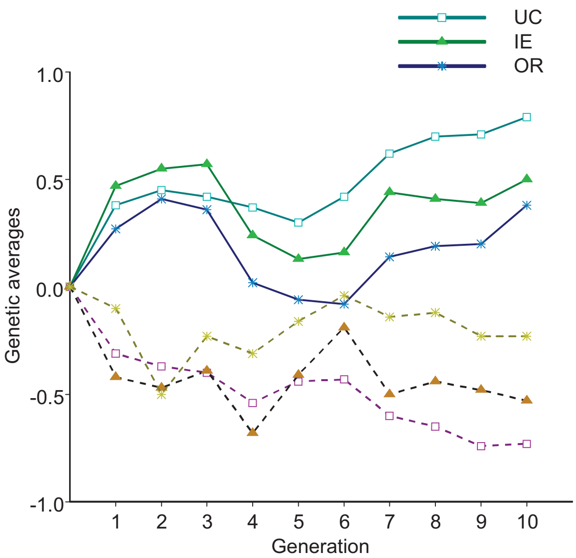

Figure 3. Genetic trends of uterine capacity (UC), ovulation rate (OR), and number of implanted embryos (IE) for high and low lines.

as a possible candidate to improve litter size in rabbits: higher heritability, relatively high genetic correlation, absence of fetal migration, and high litter sizes when only one uterine horn is functional (see Argente et al., 2000[a]), a phenomenon that is completely different in pigs or mice.

ACKNOWLEDGEMENTS

This experiment was supported by CICYT AGF98-0382

REFERENCES

ARGENTE, M. J., SANTACREU M. A., CLIMENT A. AND BLASCO A., 2000. Genetic correlations between litter size and uterine capacity. 7th World Rabbit Congress. Valencia, 4-7 July 2000.

ARGENTE, M.J., HALEY C.S., VISSCHER P.M., BLASCO A., 2000. Analyses for the presence of a major gene affecting uterine capacity in unilaterally ovariectomized does. 7th World Rabbit Congress. Valencia, 4-7 July 2000.

ARGENTE, M.J.,. SANTACREU M. A., CLIMENT A., BLASCO, A. AND BOLET G., 1997 Divergent selection for uterine efficiency in rabbits. J. of Anim. Sci. **75:** 2350 - 2354.

BLASCO, A, 1996 Genetics of litter size and does fertility in the rabbit. 6th World Rabbit Congress. Toulouse, 1996. **2:** 219-228.

BLASCO, A., BIDANEL J. P. , BOLET G. , HALEY C. AND SANTACREU M. A. , 1993 The genetics of prenatal survival of pigs and rabbits: a review. Livestock Prod. Sci. **37:**1-21.

BLASCO, A., ARGENTE M. J. , HALEY C. AND SANTACREU M. A. , 1994 Relationships between Components of Litter Size in Hemiovariectomized and Intact Rabbit Does. J Anim. Sci. **72:** 3066-3072.

BLASCO A., SORENSEN D., BIDANEL J.P. 1998. A Bayesian analysis of genetic parameters and selection response for litter size components in pigs. *Genetics*. 149: 301-306.

BOLET, G., SANTACREU M. A., ARGENTE M. J, CLIMENT A. AND BLASCO A., 1994 Divergent selection for uterine efficiency in unilaterally ovariectomized rabbits. I. Phenotypic and genetic parameters. 5th World Congress on Genetics Applied to the Livestock Production. Guelph, 1994. **19:** 261-264.

GION, J. M., CLUTTER A. C. AND NIELSEN M. K., 1990 Alternative methods of selection for litter size in mice: II Response to thirteen generations of selection. J. Anim. Sci. **68:** 3543-3556.

GROENEVELD E., 1994. VCE- A multivariate multimodel REML (co)variance component estimation package. 5th World Congress on Genetics applied to animal production, Guelph, August 7-12 ,1994, 22, 47.

KIRBY, Y. L., KOCHERA I. AND NIELSEN M.K., 1993 Alternative methods of selection for litter size in mice: III. Response to 21 generations of selection. J. Anim. Sci. **71:** 571-578.

MOCE L., PILES M., SANTACREU M. A. AND BLACO A., 2000. Correlated response to selection for uterine capacity on teat number and effect of teat number on survival rate. 7th World Rabbit Congress. Valencia, 4-7 July 2000.

SANTACREU, M. A., VIUDES, P., AND BLASCO, A. 1990. Evaluation par coelioscopie des corps jaunes et des embryons. Influence sur la taille de portée chez la lapine. *Reproduction, Nutrition, Development*. 30: 583-588.

SANTACREU, M. A., ARGENTE M. J., MOCÉ M.L.. AND BLASCO A., 2000. Selection for uterine capacity. II Response to selection estimated with a cryopreserved control population. 7th World Rabbit Congress. Valencia, 4-7 July 2000.