GENETICS OF LITTER SIZE AND DOES FERTILITY IN THE RABBIT

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INTRODUCTION

Litter size is a more important trait in rabbit production than in other prolific species (BASELGA and BLASCO, 1989; ARMERO and BLASCO, 1992). Current genetic schemes for rabbit meat production are based in a three way cross, in which two lines are selected for litter size in order to produce the crossbred doe and other line is selected for growth rate in order to produce terminal sires. After the gigantic review of ROCHAMBEAU (1988) for the Budapest World Rabbit Congress, there has not been any similar compilation of all the literature about the experiments performed in rabbit genetics. The present review has a more modest scope and it will be concentrated in the genetics of litter size and its components. With some exception, only the experiments performed since 1988 have been included in this review, and only rabbit for meat production has been considered. A review of the experiments of selection for growth rate can be found in BLASCO (1995), and all the topics related to molecular genetics will be found in other review paper of this Congress.

GENETIC PARAMETERS

There is a wide consensus for giving low values to the heritability of litter size of all prolific species, generally under 0.10, and the same can be said about the environmental permanent effects of litter size. The work done since 1988 has not modified this situation (UTRILLAS *et al.*, 1991; BASELGA *et al.*, 1992; FERRAZ *et al.*, 1992; FERRAZ and ELER, 1994, 1996; ROCHAMBEAU *et al.*, 1994; LUKEFAHR *et al.*, 1996; GOMEZ *et al.*, 1996). The high values obtained by KHALIL *et al.* (1989), BLASCO *et al.* (1993b) and KROGMEIER *et al.* (1994) cannot be taken seriously due to their high standard errors. Genetic maternal effects seem to be irrelevant (FERRAZ *et al.*, 1992; GOMEZ, 1994;), and the whole maternal effects account for less than a 10% of the phenotypic variation (FERRAZ *et al.*, 1992; GOMEZ, 1994; KROGMEIER *et al.*, 1994).

Genetic correlations between growth and reproductive traits seem to be low (MGHENI and CHRISTENSEN, 1985; CAMACHO and BASELGA, 1990), which agrees with results in pigs (DUCOS and BIDANEL, 1996), but nor in mice (see BRIEN, 1986 for a review). Nevertheless, although all genetic parameters depend on the population in which they are measured, genetic correlations are more sensitive for comparisons, since they are sensitive to changes in the gene frequencies and genetic disequilibrium bias the estimates, mainly if the genetic variances are low.

Relevant maternal heterosis effects for litter size, usually between 10% and 15%, and some small direct heterosis effects have been detected many years ago in pigs and rabbits. The more recent work in this area agrees with these previous results (BRUN *et al.*, 1992; BRUN, 1993; KHALIL *et al.*, 1995; LUKEFAHR *et al.*, 1996; NOFAL *et al.*, 1996). The high direct heterosis found by SZENDRO *et al.* (1996) is probably due to a sampling effect, given the small size of the experiment. As the heterotic effects depend on how closed are the populations being crossed, all generalisations should be taken with caution.

DIRECT SELECTION ON LITTER SIZE

Only two of the experiments cited by ROCHAMBEAU (1988) are still being carried out. These experiments are performed by the Station d'Amélioration Génétique des Animaux of Toulouse (SAGA, INRA, France) and by the Universidad Politécnica de Valencia (Spain). Recently, the Institut de Recerca y Tecnologia Alimentaria (IRTA, Barcelona, Spain) has started a program closely linked to the Valencia program, and they present their first results in this congress. No results from other programs of selection for litter size have been published, apart from a paper by NIEDZWIADEK *et al.* (1992). This last paper does not clearly establish the method of selection, and the results do not include a comparison with a control population or other method to separate environmental from genetic effects, thus it is not possible to know which part of the progress that the authors claim to have obtained is due to an improvement of the environment, or even if some genetic progress has been obtained at all.

The results of the French laboratory have been published by ROCHAMBEAU *et al.* (1994) and POUJARDIEU *et al.* (1994). Selection is performed in two synthetic lines by means of an index including data of the female, mother, full and half sisters. The selection criterion is litter size at birth in one line and litter size at weaning in the other one. The lines have an average of 84 and 121 does respectively. Although they have a control unselected population, ROCHAMBEAU *et al.* (1994) used the BLUP/REML technique to evaluate the genetic progress. After 18 generations of selection, the authors find a progress of almost three young rabbits in both lines when the genetic progress is evaluated by BLUP/REML. However, the difference between control and selected population is around one young rabbit, which means 0.06 rabbits per generation, which agrees with the experiment of BRUN (1993), who compared the results of the hybrid does produced by crossing the control line with a line called B, with another hybrid doe produced by crossing line B with the selected line after 13 generations of selection, and a difference of 0,7 to 0.9 weaned rabbits was obtained.

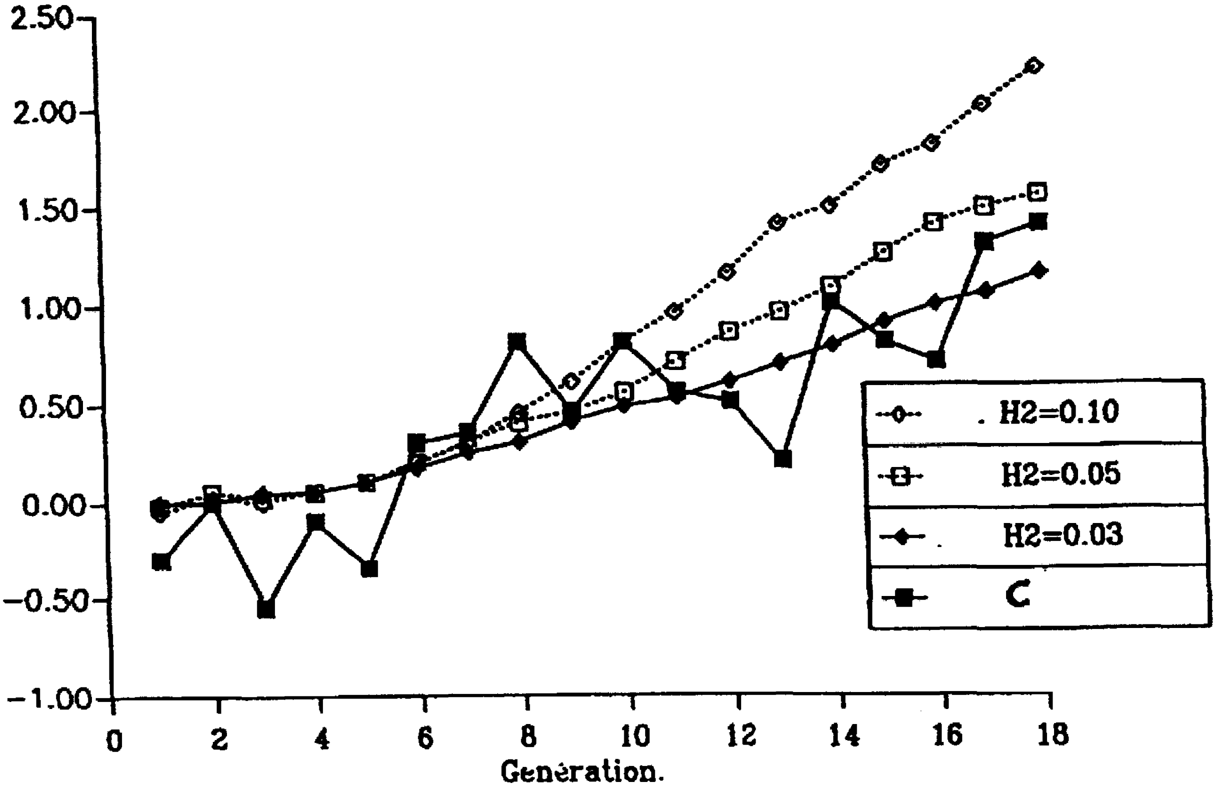
The reasons of this disparity lay in the way of estimating the response of selection by the BLUP/REML method. As this is a standard method used nowadays, and the other experiment of selection has also used this method for estimating the response to selection, it will deserve a comment.

Control populations are needed in order to separate genetic from environmental effects. The main problem of their use is that genetic drift augments the variance of the response, and after many generations, control populations become less and less useful. Besides, if selection has been successful, some interaction between genotype and environment can distort the results; for example, it is expected that the environment will affect in a different way a very prolific selected line in comparison to a less prolific control. A large part of all of these inconveniences is being removed by the modern use of frozen control populations. Embryos of generation 0 are frozen and later thawed and transferred to does in order to produce a control population contemporary of selected animals of generation n. There is still a problem in the case of reproductive traits: they are highly variable, and the farm facilities available to obtain data are usually quite limited. The response is then estimated by comparing the averages of selected and control populations at generation n, and this difference has usually a high standard error.

BLUP/REML techniques consists in predicting the genetic values by BLUP, by using REML estimates of the genetic variances in the mixed model equations. The estimated genetic values are no longer BLUP, but the method presents good statistical properties (see, for example, GIANOLA and FERNANDO., 1986). However, it has a major inconvenience: the results of the estimation are strongly dependent on the genetic values provided by the REML estimates (THOMPSON, 1986; SORENSEN and JOHANSSON, 1992). This means the estimated response will be higher or lower, depending on the estimated values of the genetic parameters (see figure 1, taken from POUJARDIEU *et al.*, 1994). When comparing this method with the use of control populations, a main difference to be found is that a control population provides information which is independent on the model used. Whether there are dominance, major genes or other alterations of the genetic selection process, a control population will allow to differentiate between genetic and environmental effects, whereas BLUP/REML estimates are dependent on the model used to estimate the genetic parameters and genetic values. The additive model is normally used, and it could not be satisfactory for litter size analyses. For example, it is well known that the genetic determination of litter size has some dominance effect.

There is another problem related to the precision of the results. A regression line through the average genetic values per generation is often used to represent the "genetic trend". This method could fit better in the case of overlapping generations processes than when selection is performed in discrete generations. If generations are discrete, each process of selection has its own peculiarities that make the genetic progress non-linear. For example, the selection pressure is often different from generation to generation, the Bulmer effect and the reduction of the variance with selection makes the process less efficient, natural selection decreases the efficiency of selection for litter size through an increment of inbreeding, etc. Besides, the error of this coefficient of regression is often much lower than the error of the response, because it does not include the error due to genetic drift and the estimation errors of the genetic parameters that were used to predict the genetic means per generation. The genetic drift error can be very important when many generations are considered, and the error of the genetic parameters estimates is large in small and even medium-size samples.

Figure 1 : Genetic trends of litter size evaluated by BLUP/REML using different heritabilities (H2), and using a control (C) population (from POUJARDIEU *et al.*, 1994)



For the reasons exposed above, the response estimated with a control population is preferable than the estimates given by BLUP/REML, but when a control population is available, both techniques should be considered as complementary, and only when the results differ, the model used in the BLUP/REML analysis or the size of the control population should be questioned. The results of ROCHAMBEAU *et al.* (1994) from the control population comparison corresponds to a heritability extremely low (0.03, POUJARDIEU *et al.*, 1994), but they agree with results of the selection experiments performed in the Valencia laboratory as we will see now.

The results of the Valencia experiment have been published by ESTANY *et al.* (1989) and BASELGA *et al.* (1992). Selection is performed in two lines (A and V), by and index similar to the French index (line A) and by a BLUP on a repeatability animal model (line V). Both lines are selected on number of weaned rabbits. No control population is available. After 11 generations of selection in line A and 8 in line V, the genetic progress estimated by BLUP/REML was 0.10 and 0.03 rabbits per generation respectively (BASELGA *et al.*, 1992).

The results of the other Spanish experiment, carried out by IRTA, are published in this Congress by GOMEZ *et al.* (1996). They have selected a synthetic line for litter size at weaning with overlapping generations during three years. They found a genetic progress, estimated by BLUP/REML, of 0.09 rabbits per year. As the average life of a male and a females was around 10 month (GOMEZ, personal comm.), this is equivalent to a progress of 0.11 rabbits per generation.

Table 1 : Selection experiments for litter size

Authors	Line	Selection criterion	Method of selection	Method to assess the response	N. of generations	Estimated response (rabbits/gen)
BASELGA *et al.*, 1992	A	NW	Index	REML/BLUP	11	0.10
	V	NW	BLUP	REML/BLUP	8	0.03
ROCHAMBEAU et al., 1994	A1077	NW	Index	REML/BLUP	18	0.16
	A2066	NBA	Index	REML/BLUP	18	0.15
POUJARDIEU *et al.*, 1994	A2066			CONTROL		0.06
GOMEZ *et al.*, 1996	P	NW	BLUP	REML/BLUP	3	0.11

NW: Number of weaned rabbits. NBA: Number of born alive

These results are deceptive and show how difficult is to select for litter size. However, the expected response calculated by simple formulae is relatively high, around 0.30 rabbits per generation, due to the high coefficient of variation of litter size, as SMITH (1984) emphasised. The causes of this disagreement between theory and practice have been examined by GOMEZ (1994) and GOMEZ *et al.* (1994), who shows that if less simple models are used to calculate the expected response (taking into account inbreeding, Bulmer effect, and a correlation between parities less than one), the calculated expected response is not so far from the obtained one. These difficulties in improving litter size have also been emphasised in pigs (see HALEY *et al.*, 1988, and BLASCO *et al.*, 1995, for reviews). This situation has lead to several alternative proposals to improve litter size, that will be examined in this review. Nevertheless, BRUN (1993) has called the attention to the improvement of the litter size at birth of the hybrids of the French program. In three experiments carried out in 1970-72, 1979-80 and 1987-89, litter size of the hybrids was 7.9, 8.0 and 9.7. As there was no control population, these results are not strictly comparable, since the improvement could come from an improved environment, but it is also possible that the genes for litter size in selected lines are matched by the decreasing performance produced by inbreeding. If so, when crossing the selected lines, the effect of inbreeding disappears and genes for litter size would produce better litters. A higher heterosis is also expected as a consequence of the higher consanguinity of the selected lines.

INDIRECT SELECTION FOR LITTER SIZE

Selection for ovulation rate and prenatal survival

A way of selecting for litter size could be to select a correlated trait with a higher heritability. Although this seems reasonable, there are homeostatic mechanisms that often match the progress obtained by selection. For example, selection for ovulation rate has been proved to be inefficient to increase litter size in mice and pigs, since a correlated decrease in prenatal survival accompanied the increase obtained in ovulation rate (see BLASCO *et al.*, 1993a for a review). Prenatal survival seems to have a low heritability, and it is not a candidate to substitute selection for litter size, although some success was obtained in mice, but not in pigs (see BLASCO *et al.*, 1995 for a review). Selection for an index including ovulation rate and litter size has been successful to improve litter size in mice (CLUTER *et al.*, 1990) and pigs (CASEY *et al.*, 1994). In mice, it was as efficient as direct selection for litter size. In pigs, the results of Casey et al., 1994 are complicated by the method of selection, an index of ovulation rate and embryonic survival which requires surgical intervention, but CASEY *et al.* (1995) showed a significant genetic progress in their last generation of selection in which no surgical intervention happened.

Given the experience of pigs and mice, an index of selection for ovulation rate and prenatal survival could be a reasonable alternative for selection on litter size in rabbit. The method is based in considering litter size as an index of selection with suboptimal economic weights. Litter size (LS) can be expressed as a product of ovation rate (OR) and prenatal survival (PS)

$$LS = OR \, . \, SP$$

If a linear index is used to select for OR and PS, LS can be considered as a profit function that should be maximised. Then, the economic weights for OR and PS are

$$a_{OR} = \left[\frac{\delta TC}{\delta OR}\right]_{\substack{OR=\overline{OR}\\ SP=\overline{SP}}} = \overline{SP} \; ; \quad a_{SP} = \left[\frac{\delta TC}{\delta SP}\right]_{\substack{OR-\overline{OR}\\ SP-\overline{SP}}} = \overline{OR}$$

When the genetic and phenotypic correlations are the same, and the heritabilities of both traits are also the same, the linear index becomes

$$I = h^2\left(\overline{SP} \cdot OR + \overline{OR} \cdot SP\right)$$

but a Taylor expansion of the expression for LS gives the same index:

$$LS = OR \cdot SP = \overline{SP} \cdot OR + \overline{OR} \cdot SP$$

then, to select by an index is the same as directly selecting for LS when the genetic and phenotypic correlations are the same, and the heritabilities of both traits are also the same.

There is only one published experiment about heritability of OR and PS in rabbit. In this experiment the genetic and phenotypic correlations between OR and PS were -0.14 and -0.30 respectively, and the heritabilities of OR and PS were 0.21 and 0.23 (BLASCO *et al.*, 1993b). With this evidence, it seems hazardous to start an experiment of selection by using an index based on the litter size components.

Selection for uterine efficiency

Selection on uterine capacity was suggested by CHRISTENSON *et al.* (1987) as an alternative method to improve litter size in pigs. The concept of uterine capacity was introduced in the literature by BAZER *et al.* (1969), who suggested that the competence of the foetuses for a limiting factor before and during implantation could explain a large part of the observed prenatal mortality. Later, CHRISTENSON *et al.* (1987) defined uterine capacity as the maximum number of foetuses that an uterus can carry out with success, when the number of ova shed is not a limiting factor. DZIUK (1968) and CHRISTENSON *et al.* (1987) suggested use of unilateral ovariectomy and hysterectomy to measure uterine capacity in pigs. Removing one ovary produces a duplication of the ovulation rate in the other ovary, leading to an overcrowding of embryos in the remaining uterine horn. In rabbits, unlike in pigs, transuterine migration is almost never found (BLASCO *et al.*, 1994), thus only unilateral ovariectomy is needed (FLEMING *et al.*, 1984; BLASCO *et al.*, 1994). Another advantage of rabbits is that it is possible to observe the corpora lutea and implantation sites by laparoscopy without damaging litter size (SANTACREU *et al.* 1990). This is particularly important, since uterine capacity would depend on two traits: number of implanted embryos and survival after implantation.

Only results from two selection experiments in rabbits and one selection experiment in mice have been hitherto published. In mice, KIRBY and NIELSEN (1993) have shown that uterine efficiency 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, as we have seen before.

The experiments of selection for uterine efficiency in rabbits were performed in the SAGA of Toulouse and the Universidad Politécnica de Valencia. Both were divergent selection experiments, but the criterion of selection was different. In one of the experiments, selection was made on litter size, which includes the two components of uterine capacity (number of implanted embryos and survival after implantation), and in the other experiment selection was performed on number of dead foetuses from implantation to birth, which concentrates on foetal survival. The results have been published by BOLET *et al.* (1994, 1996), SANTACREU *et al.* (1994) and ARGENTE *et al.* (1996a), and they are summarized in figure 2. It can be concluded that number of dead foetuses from implantation to birth did not change in neither of the experiments, but litter size changed in the Valencia experiment, in which litter size was the selection criterion. The divergence in litter size in this experiment seems to be associated to a divergence in number of implanted embryos more than to differences in foetal survival, showing that it was the competence among embryos before implantation which lead to this increment in litter size. ADAMS (1962) and HAFEZ (1964) suggested that competence among embryos could produce differences in foetal survival when the rate of implanted embryos is high. However, from these results it seems that this competence is not a main factor in determining it.

Several hypothesis are underlying in the experiment with unilaterally ovariectomized rabbits, and they have been discussed by BOLET *et al.* (1996). The most relevant one is whether selection on uterine efficiency in does with only one functional uterine horn will be efficient to improve litter size in females with both horns being functional. Argente et al. (1996b) gives some complementary results of experiment 2, showing that females of the line selected to increase litter size, with both uterine horns being functional, still have a rabbit more than females of the other divergent line.

Figure 2 : Selection for uterine efficiency. Experiment1: SAGA, INRA, Toulouse.
Experiment 2: Universidad Politécnica de Valencia..
From SANTACREU *et al.* (1994).

Evolution of the difference between high and low selection lines in sitter size (LS), number of corpora lutea (CL), number of implanted embryos (IE), and number of dead fetuses between implantation and birth (ND), (figure a) and embryo, fetal and prenatal survival (ES, FS, PS), (figure b), from generation 0 (G0) to generation 4. Experiment 1. Selection to decrease (high line) and increase (low line) ND.

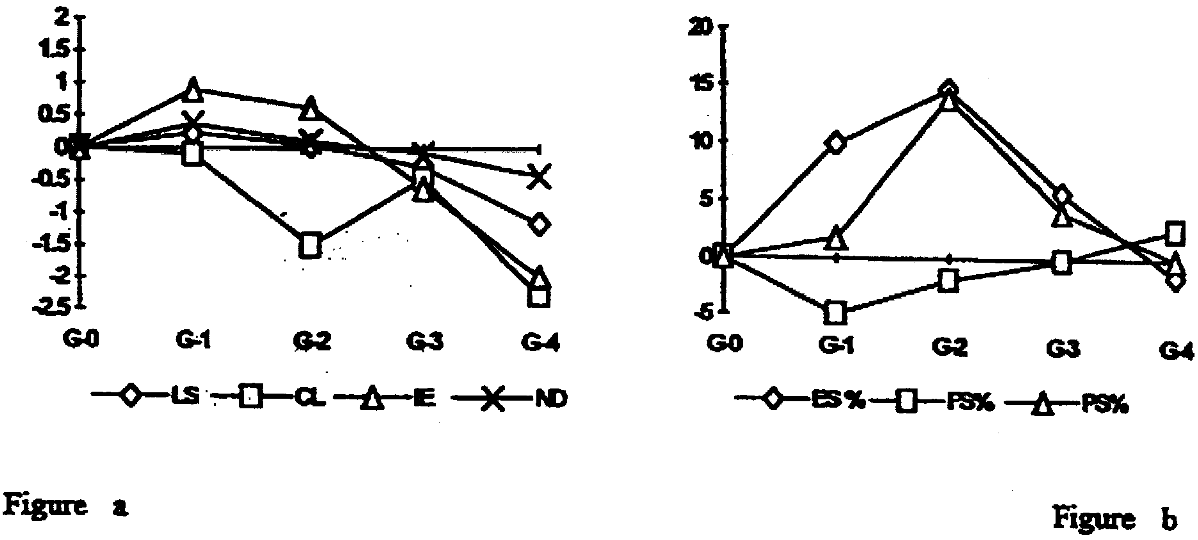


Figure a

Figure b

Evolution of the difference between high and low selection lines in litter size (LS), number of corpora lutea (CL), number of implanted embryos (IE), and number of dead fetuses between implantation and birth (ND), (figure a) and embryo, fetal and prenatal survival (ES, FS, PS) (figure b), from generation 0 (G0) to generation 4. Experiment 2. Selection to decrease (high line) and dicrease (low line) LS.

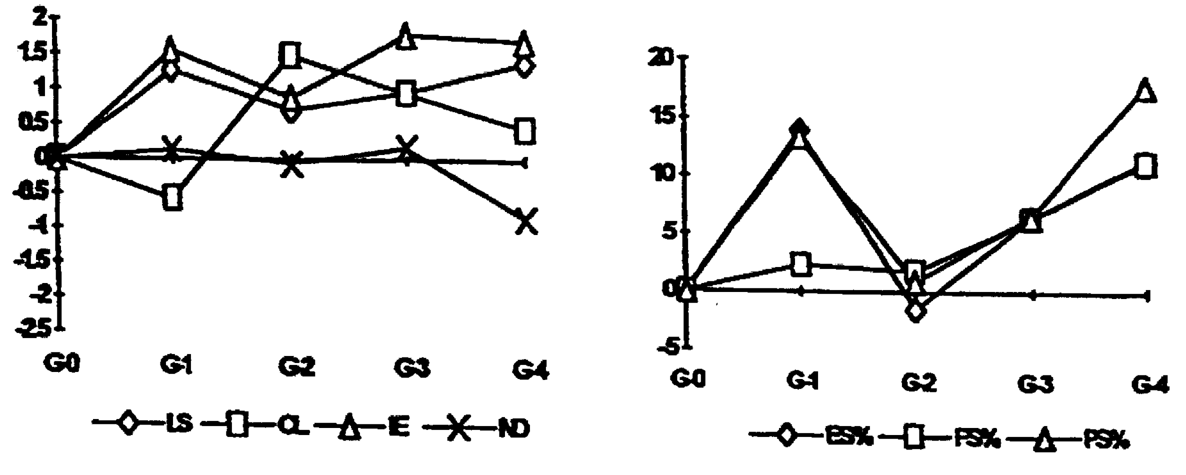


Figure a

Figure b

The improvement in number of implanted embryos can be due to differences in rate of fecundation, embryo survival or factors related to the uterus. Fecundation rate seems to be very high in intact rabbits though varying between strains (ADAMS, 1960; BOLET and THEAU-CLEMENT, 1994). There are not differences in fecundation rate between intact and unilaterally ovariectomized lines (SANTACREU *et al.*, 1996), therefore the differences in number of implanted embryos shall be at least attributed to differences in embryo viability related to the embryo (vgr. chromosomic abnormalities) or the uterus environment, i.e. the amount and composition of uterine secretions. As chromosomic abnormalities are rare in rabbits (FECHHEIMER and BEATTY, 1974), it seems that competition among embryos for some uterine factor before implantation has a major role to explain the differences in uterine efficiency.

HYPERPROLIFIC SCHEMES

LEGAUT and GRUAND (1976) suggested to take advantage of the large organisations of purebreed pigs to improve litter size by performing high pressures of selection. The offspring of hyperprolific females is used to constitute a line called "hyperprolific" that can be used in the current crossbreeding scheemes. This system has proved to be successful in pigs (HERMENT *et al.*, 1994) and it is now applied by private pig companies. The same system has now been established in the nucleus of selection linked to the Universidad Politécnica of Valencia, taking advantage of the possibility of freezing embryos of the hyperprolific females. The process is described in García et al. (1996). When a doe of one of the nucleus has more than 16 born alive in the first parity, or 28, 41 and 53 in the sum of parities 2nd, 3rd and 4th, then it is mated with the best males of the selection nucleus, according their BLUP evaluation, and the embryos produced are frozen and kept until there are enough to constitute a hyperprolific population. The size of the offspring in several parities was calculated to have donor does of the same genetic value. A first evaluation shows that this line has 1.5 ova more than the lines of the selection nucleus (Cifre et al, 1994), although no differences for litter size have been found until now (CIFRE *et al.*, 1996).

THE CONSEQUENCES OF SELECTION

Direct or indirect selection will produce at court or long term lines of high prolificity. It is often discussed whether this would produce some undesirable effects, like a higher mortality at birth or at weaning. When the selection criterion is litter size at weaning, the criterion takes into account the ability of the mother for littering, but if selection is performed on litter size at birth, it is a reasonable question whether mortality will increase from birth to weaning. There is also a problem related to the definition of litter size at birth. The more logical criterion for selection seems to be number of born alive instead of total number born, but there is some inaccuracy when evaluating the number of born alive, since some delay can happens between the birth and the control, and some of the number of dead rabbits could have dye just before the control was taken.

The genetic correlation between total litter size at birth and number of born alive is near unity (KROGMEIER *et al.*, 1994). However, although no data have been published in rabbits, in pigs BLASCO *et al.* (1995) have called the attention upon a higher number of dead piglets found in the experiments that claimed to have had success when selecting for litter size. As expected, the number of dead born increased in all the experiments. The important result is that this increment was not totally due to a scale factor (i.e., if total number of born increases, both born alive and dead will increase proportionally) but it was higher than expected.

Although number of born alive also increased in all of these experiments, it would be convenient to decrease the number of dead born animals. The problem has not an easy solution. As BLASCO *et al.* (1995) commented, there is a difficulty in analysing genetic parameters of number of dead born, arising from the clearly non normal distribution of the trait. This leads to the question of how reliable are the genetic parameters often given for both traits, and encourages the idea of performing analyses in which the number of dead born will be considered as a categorical trait and the number of born alive as a normally distributed trait.

Another common preoccupation is whether the best animals of a nucleus will produce hybrids that will be the best in a commercial farm. The interactions genotype per environment have not been evaluated in rabbit, with the exception of some indirect approach to detect interactions produced by type of food (BRUN and LEBAS, 1994). These results and the results of some recent studies in pigs (BIDANEL and DUCOS, 1995), suggest that interaction genotype per environment has been overevaluated, and it is not important when all data are analysed properly. Nevertheless it has to be stated that very prolific animals should not be reared in hard environments. Selection programs are normally prepared for intensive production, which is performed in rather standard conditions, therefore farms suffering of poor environment should first invest in improving the rearing conditions than in high genetic quality animals.

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REFERENCES

ADAMS C.E., 1960. Studies on prenatal mortality in the rabbit, orictolagus cuniculus: the amount and distribution of loss before after implantation. *J. Endocrin.* **19**, 325-344.

ADAMS C.E., 1962. Studies on prenatal mortality in the rabbit, orictolagus cuniculus: the effect of transferring varying numbers of eggs. *J. Endocrin.* 24:471-490.ARMERO, Q.; BLASCO, A. 1992. Economic weights for rabbit selection indices. *V World Congress on cuniculture*. Corvallis, Oregon, 1992. **Vol. A**, 637-642.

ARGENTE M.J., SANTACREU M.A., CLIMENT A., BLASCO A., BOLET G., 1996a. Divergent selection for uterine efficiency in rabbits. II. Direct and indirect responses to Selection. *Journal of Animal Science* (Submited).

ARGENTE M.J., SANTACREU M.A., CLIMENT A., BLASCO A., 1996b. Selection for uterine efficiency in rabbits. *6th World Rabbit Congress*. Toulouse, 1996.

BASELGA M., BLASCO A., 1989. Mejora Genética del Conejo de producción de carne. *Mundi-Prensa*. Madrid, 110 pp.

BASELGA M., GOMEZ E., CIFRE P., CAMACHO J., 1992. Genetic diversity of litter size traits between parties in rabbits. *Proc. V World Rabbit Congress* **vol. A**, 198-205.

BAZER F.W., CLAWSON A.J., ROBISON O.W., ULBERG L.C., 1969. Uterine capacity in gilts. *J. Reprod. Fert.* **18**, 121-124.

BIDANEL J.P., DUCOS A., 1995. Corrélations génétiques entre les caractères mesurés dans le stations publiques et en élevages dans les races porcines Large White et Landrace Francais. 27èmes Journées de la Recherche Porcine en France. Paris, février, 1995. 143-148.

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

BLASCO A., SANTACREU M.A, THOMPSON R., HALEY C.S., 1993b. Estimates of genetic parameters for ovulation rate, prenatal survival and litter size in rabbits from an elliptical selection experiment. *Livestock Production Science* **34**, 163-174.

BLASCO A., ARGENTE M.J., HALEY C.S., SANTACREU M.A., 1994. Relationships between components of litter size in unilaterally ovariectomized and intact rabbit does. *Journal of Animal Science* **72**, 3066-3072.

BLASCO A., BIDANEL J.P., HALEY C.S., 1995. Genetics and neonatal survival. *In:The neonatal pig. Development and survival.* M.A. Varley (Ed.) C.A.B. International.

BLASCO A., 1995. Estado actual de la investigación en mejora genética del conejo de producción de carne. *VII. Jornadas Técnicas sobre cunicultura.* Expoaviga 95. Barcelona, 1995, 50-63.

BOLET G., THEAU-CLEMENT M., 1994. Fertilisation rate and preimplantion embryonic development in two rabbit strains of different fecundity, in purebreeding and crossbreeding. *Anim. Reprod. Sci.* **36**, 153.

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

BOLET G., ARGENTE M.J., SANTACREU M.A., CLIMENT A., BLASCO A., 1996. Divergent selection for uterine capacity in rabbits. Y. Genetic and phenotypic parameters. *J. Anim. Scie* (Submited).

BRIEN F.D., 1986. a review of the genetic and phisilogical relationships betweeen growth and reproduction in mammals. *Anim. Breed. Abstr.* **54**, 775-779.

BRUN J.M., BOLET G., OUHAYOUN J., 1992. The effects of crossbreeding and selection on productive and reproductive traits in traits in a triallel experiment between three strains of rabbits. *J. Appl. Rabbit Res.* **15**, 181-189.

BRUN J.M., 1993. Paramètres du croisement entre 3 souches de lapin et analyse de la réponse à une sélection sur la taille de portée: caractères des portées à la naissance et au sevrage. *Genetic, Selection and Evolution* **25**, 459-474.

BRUN J.M., LEBAS F., 1994. Etude préliminaire des interactions entre l'origine paternelle et le régime alimentaire des lapines sur leurs performances de reproduction. *6èmes journées de la recherche cunicole*. La Rochelle. 1994. **Vol 1**, 195-202.

CAMACHO J., BASELGA M., 1990. Genetic correlation between reproductive and growth traits in rabbits. *4th World Congress on Genetics Applied to the Livestock Production*. Edinburgh, 1990. XVI: 366-369.

CASEY D., RATHJE T.A., JOHNSON R.K., 1994. Response to ten generations of index selection for components of litter size in swine. *Proc. 5th. World Congress on Genetics Applied to Livestock Production* **vol. 17**, 315-318. Guelph, Ontario, Canada. August 1994.

CASEY D., RATHJE T., JOHNSON R.K., 1995. Index selection for components of litter size. *Nebraska Swine Report* 1995.

CIFRE J., VICENTE J.S., BASELGA M., GARCIA-XIMENEZ F., 1994. Ovulation rate in lines of rabbits selected on different criteria. Options Mediterrannéennes **8**, 247-250.

CIFRE J., BASELGA M., GARCIA-XIMENEZ F., VICENTE J.S., 1996. A study of reproductive and growth traits of a maternal rabbit line founded by selection of hyperprolific does. *6th World Rabbit Congress*. Toulouse, 1996.

CHRISTENSON R.K., LEYMASTER K.A., YOUNG L.D., 1987. Justification of unilateral hysterectomy-ovariectomy as a model to evaluate uterine capacity in swine. *Journal of Animal Science* **65**, 738-744.

CLUTTER A.C., NIELSEN M.K., JOHNSON R.K., 1990. Alternative methods of selection for litter size in mice: Y. Characterization of base population and development of methods. *J. Anim. Scie.* **68**, 3536-3542.

DUCOS A., BIDANEL J.P., 1996. Corrélations génétiques entre caractères de production et de reproduction mesurés en élevage dans le races porcines Large White et Landrace Francais. *28èmes Journées de la Recherche Porcine en France. Paris, février*, 1996. 15-21.

DZIUK P.J., 1968. Effect of number of embryos end uterine space on embryo survival in the pig. *J. Anim. Sci.* **27**, 673-676.

ESTANY J., BASELGA M., BLASCO A., CAMACHO J., 1989. Mixed model methodology for the estimation of genetic response to selection in litter size of rabbits. *Livestock Production Science* **21**, 67-75.

FECHHEIMER N.S., BEATTY R.A., 1974. Chromosomal abnormalities and sex ratio in rabbit blastocyst. *J. Reprod. Fert.* **37**, 331-341.

FERRAZ J.B.S., JOHNSON R.K., VAN VLECK L.D., 1992. Estimation of genetic trends and genetic parameters for reproductive and growth traits of rabbits raised in subtropics with animal models. *Proc. V World Rabbit Congress* Corvallis, 1992. **vol. A**, 131-142.

FERRAZ J.B.S., ELER J.P., 1994. Use of different animal model in prediction of genetic parameters of 23 traits of Californian and New Zealand White rabbits raised in tropics and suggestion of selecction criteria. *Proc. 5th. World Congress on Genetics Applied to Livestock Production* **vol. 20**, 348-351. Guelph, Ontario, Canada. August 1994.

FERRAZ J.B.S., ELER J.P., 1996. Comparison of animal models for estimation of (co)variance components and genetic parameters of reproductive, growth and slaughter traits of Californian and New Zealand White rabbits under tropical conditions. *6th World Rabbit Congress*. Toulouse, 1996.

FLEMING M.W., RHODES, R.C., DAILEY R.A., 1984. Compensatory responses after unilateral ovariectomy in rabbits. *Biol. Reprod.* **30**, 82-86.

GARCIA-XIMENEZ F., VICENTE J.S., CIFRE J., BASELGA M., 1996. Foundation of a maternal rabbit line using hysterectomie and embryo cryopreservation. *6th World Rabbit Congress.* Toulouse, 1996.

GIANOLA D., FERNANDO R.L., 1986. Bayesian methods in animal breeding theory. *J. Anim. Sci.* **63**, 217-244.

GOMEZ E., 1994. La selección del tamaño de camada en el conejo de carne: influencia de los efectos maternos y de la heterogeneidad genetica entre partos. *Tesis Doctoral.* Universidad Politécnica de Valencia. Valencia. Spain.

GOMEZ E., BASELGA M., CIFRE P., 1994. The influence of genetic diversity between parities in selection for litter size in rabbits. *Proc. 5th. World Congress on Genetics Applied to Livestock Production* **vol. 19**, 253-256. Guelph, Ontario, Canada. August 1994.

GOMEZ E.A., RAFEL O., RAMON J., BASELGA M., 1996. A genetic study of a line selected on litter size at weaning. *6th World Rabbit Congress.* Toulouse, 1996.

HAFEZ E.S.E., 1964. Effects of over-crowding in utero on implantation and fetal development in the rabbit. *J. Exp. Zool.* **156**, 269-287.

HALEY C.S., AVALOS E., SMITH C., 1988. Selection for litter size in the pig. *Animal Breeding Abstracts.* **56**, 317-322.

HERMENT A., RUNAVOT J.P., BIDANEL J.P., 1994. Une nouvelle évaluation de l'intérêt de la voie Hyperprolifique chez le porc. *26émes Journées de la Recherche Porcine en France. Paris.* 315-320.

KHALIL M.H., AFIFI E.A., KADRY A.E.H., 1989. Genetic analysis of weight of doe rabbits during gestation and its phenotypic relationship with reproductive efficiency at kindling. *J. of Applied Rabbit Research,* **vol 12**, 45-51.

KHALIL M.H., AFIFI E.A., YOUSSEF Y.M.K., KHADR A.E., 1995. Heterosis, maternal and direct genetic effects for litter performance and reproductive intervals in rabbit crosses. *World Rabbit Scie.* **3(3)**, 99-105.

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

KROGMEIER D., DZAPO V., MAO I.L., 1994. Additive genetic and maternal effects on litter traits in rabbits. *J. Anim. Breed. Genet.* 420.

LEGAULT C., GRUAND J., 1976. Amélioration de la prolificité des truies par la création d'une lignée "hyperprolifique" et l'usage de l'insémination artificielle: principe et résultats expérimentaux préliminaires. *8èmes Journées de la Recherche porcine en France.* Paris, février 1976, 201-206.

LUKEFAHR S.D., CHEEKE P.R., PATTON N.M., 1996. Heredability of milk production and 21-day litter weight and litter size in purebred and crossbred rabbits using an animal model. *6th World Rabbit Congress.* Toulouse, 1996.

MGHENI M., CHRISTENSEN K., 1985. Selection experiment on growth and litter size in rabbits. III. Two-way selection response for litter size. *Acta Agric. Scand.* **35**, 287-294.

NIEDZWIADEK S., FIJAL J., BIELANSKI P., 1992. Progress in area of reproduction in a specialized line of rabbits. *Proc. V World Rabbit Congress* **vol. A**, 314-321.

NOFAL R.Y., TÓTH S., VIRÁG GY., 1996. Evaluation of seven breed groups of rabbits for litter traits. *6th World Rabbit Congress.* Toulouse, 1996.

POUJARDIEU B., GUICHARD F., ROCHAMBEAU H. de, ROUVIER R., 1994. Le modèle animal application au lapin et aux palmipèdes. *Proc. Séminaire Modele Animal* 143-150. La Colle sur Loup, France. Septembre 1994.

ROCHAMBEAU H. de, 1988. Genetics of the rabbit for wool and meat production. *Proc. 4th. World Rabbit Congress.* **vol. 2**, 1-68. Budapest, Hungary. October, 1988.

ROCHAMBEAU H de, BOLET G., TUDELA F., 1994. Long term selection-comparison of two rabbits strains. *Proc. 5th. World Congress on Genetics Applied to Livestock Production* **vol. 19**, 257-260. Guelph, Ontario, Canada. August 1994.

SANTACREU M.A., VIUDES M.P., BLASCO A., 1990. Evaluation par coelioscopie des corps jaunes et des embryons. Influence sur la taille de portée chez la lapine. *Reprod. Nutr. Dev.* **30**, 583-588.

SANTACREU M.A., ARGENTE M.J., CLIMENT A., BLASCO A., BOLET G., 1994. Divergent selection for uterine efficiency in unilaterally ovariectomized rabbits. II Response to selection. *Proc. 5th. World Congress on Genetics Applied to Livestock Production* **vol. 19**, 265-267. Guelph, Ontario, Canada. August, 1994.

SANTACREU M.A., CLIMENT A., GALLEGO M., FAYOS L., BLASCO A., 1996. Fertilization rate and early embryo development in two rabbit lines selected on uterine efficiency. *6th World Rabbit Congress.* Toulouse, 1996.

SMITH S.P., 1984. Rates of genetic improvement in farm livestock. *Research and Devel. in Agric.* 1, 79-85.

SORENSEN D.A., JOHANSSON K., 1992. Estimation of direct and correlated responses to selection using univariate animal models. *J. Anim. Sci.* **70**, 2038-2044.

SZENDRÔ Z.S., BIRÓ-NÉMETH E., RADNAI Y., JENSEN N.E., KENESSEY A., 1996. The perfomance of Danish White and Pannon White purebred and reciprocal crossbred rabbits. *6th World Rabbit Congress.* Toulouse, 1996.

THOMPSON R., 1986. Estimation of realized heritability in a selected population using mixed model methods. *Genet. Sél. Evol.* **18(4)**,475-484.

UTRILLAS M., RAFEL O., RAMON J., 1991. Estudio de parámetros genéticos para caracteres reproductivos en una población de conejos. *IV Jornadas sobre producción animal. ITEA.* **vol. extra n° 11**, II, 616-618.