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SELECTION OF MATERNAL LINES: LAST RESULTS AND PROSPECTS

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ABSTRACT

The aim of this review is to discuss selection of maternal lines, to present last results and to draw research prospects. Firstly, we discuss the genetic variability of the maternal quality traits. A divergent selection experiment on uterine capacity was performed in Spain during eight generations; results put forward the hypothesis that there was a major gene affecting uterine capacity. Reproductive performance could be improved by including female fertility in a selection program but response to selection would be probably very low. Even if genetic correlation between prolificacy traits and growth traits are, in general, positive, the litter size effect, introduced in the statistical models of growth traits, is always highly significant and negative, showing the well known phenotypic relationship between litter size and weights. One spreading method for analysing female longevity data is survival analysis which allows inclusion of both censored and uncensored records of animals. Development of computer programs has made it possible to estimate the genetic potential of does for a longer productive life and to the genetic parameters for longevity. Studies have been conducted to settle adequate models of analysis and this criterion could be included in the selection objective.

Later we draw up an inventory of the 19 on going selection experiments in six different countries. Significant differences in direct genetic effects for litter size or litter weight were found. An alternative to the selection of maternal lines for crossbreeding could be the development of a multi-purpose line, through simultaneous selection for litter size and growth traits.

Finally we propose some conclusions. Selection objectives of maternal lines were directed towards a new direction: productivity is always a main point but breeding has to be sustainable. Therefore, we have to reduce young rabbits mortality, to increase doe longevity and to maintain genetic variability in selected lines.

Key words: selection, litter size, uterine capacity, growth, longevity, sustainable breeding

INTRODUCTION

The genetic session of the World Rabbit Congress had a long tradition of extended reviews (ROUVIER 1980, MATHERON AND POUJARDIEU 1984, ROCHAMBEAU 1988, BLASCO 1996). In this congress, BASELGA (2004) describes the essential elements of a programme of genetic improvement of meat rabbits. This first review points out various aspects : selection of specialised lines and crossbreeding, criteria in founding new lines, selection criteria, procedure to evaluate breeding values, response to selection in crossbreds and in purebreds and diffusion of genetic improvement to producer. The aim of this second review is to discuss selection of maternal lines, to present last results and to draw research prospects. BLASCO (1996) review is our starting point. Firstly, we discuss the genetic variability of the maternal quality traits. Later we draw up an inventory of the on going selection experiments and finally we propose some conclusions. Selection objectives of maternal lines were directed towards a new direction: productivity is always a main point but breeding has to be sustainable. Therefore, we have to reduce young rabbits mortality, to increase doe longevity and to maintain genetic variability in selected lines.

GENETIC VARIABILITY OF THE MATERNAL PRODUCTIVITY TRAITS

Components of litter size : uterine capacity and ovulation rate

A divergent selection experiment on uterine capacity was performed in Spain during eight generations (BLASCO *et al.* 2001). Does were ovariectomised unilaterally before puberty and selected for increased and decreased litter size. The response to selection led to a difference of 0.16 young rabbit per generation. The pattern of response was not linear and asymmetric. A high initial response was followed by a period where little further response was observed, and the response was greater for the Low line. A final burst of response was obtained in the last two cycles of selection. The High line showed higher ovarian weight linked to a higher ovulation rate and a greater length of the empty uterine horn (ARGENTE *et al.* 2003a). Uterine capacity was related to both blood supply and length of the uterine horn. Increasing uterine capacity increased uterine length and decreased weight of foetus and foetal placenta. Foetal survival depended mainly on the maternal genotype and the embryo genotype only affected the foetal survival only when embryo transfer was performed to a favourable maternal environment (MOCÉ *et al.* 2004). Selection for uterine capacity led mainly to modification of early embryonic survival and secondarily to modification of late survival. ARGENTE *et al.* (2003b) put forward the hypothesis that there was a major gene with large effect on implanted embryos and on embryo survival and with moderate effect on ovulation rate, foetal and prenatal survival and uterine capacity. BOSZE *et al.* (2002) pointed to the possible relation between doe genotype and the κ -casein locus and reproduction traits. There was a significant relationship between κ -casein genotype and litter size at birth. BOSZE *et al.* (2002) put forward the hypothesis of a major gene on litter size in a nearby locus. These two hypothetical genes are good candidates for a QTL mapping experiment.

Genetic parameters of fertility, litter size, young rabbit individual weight, variability of weights.

Despite of its importance on the reproductive success and therefore, on profitability and efficiency of production of farms, the information in the literature about variance components of fertility is scarce. PILES *et al.* (2004) considered fertility, defined as success or failure to natural mating, as a binary trait of the male and of the female. The authors showed that heritability of male fertility was negligible and that heritability of female fertility was low (0.6%). Genetic correlation between both traits was found to be high and positive (0.73) in one of the lines, which suggests that the genetic control of both traits could be partly the same, but this result should be confirmed given the low values of heritabilities. It seems that reproductive performance could be improved by including female fertility in a selection program but response to selection would be probably very low. Concerning litter size at different moments (birth, weaning or slaughter age), from the review by BLASCO (1996) the reported estimates of the heritability confirm the known low values, generally lower than a 15% of the phenotypic variation and, that the ratio between the variance of genetic non-additive plus permanent environmental effects and the phenotypic variance is between 10 and 20% (GOMEZ *et al.*, 1996; LUKEFAHR and HAMILTON, 2000; ROCHAMBEAU, 1998; ARGENTE *et al.*, 2003a; GARREAU *et al.*, 2000; RASTOGI *et al.*, 2000, GARCIA and BASELGA, 2002 a,b). Genetic correlations between total litter size at birth and number of young rabbits born alive are close to 1 (GARCIA and BASELGA, 2002 a,b) and genetic correlations between litter size at birth and number of rabbits weaned and between litter size at birth and number of rabbits at slaughter age are also high (0.6-0.8) and positive (GARCIA and BASELGA, 2002 a,b). Recent estimates of heterosis for litter size traits (born alive, total born and number of young weaned) also confirm previous reported values, ranging between 4 and 21% depending on the lines involved to get the crossbred does (NOFAL *et al.*, 1996; BRUN *et al.*, 1998; PRAYAGA and EADY, 2002; BASELGA *et al.*, 2003). The estimates of genetic correlation between prolificacy traits and growth traits are still limited. Despite some contradictory results given in the nineties, the most recent studies show low and, in general, positive values of these correlations (GOMEZ *et al.* 1998; GARREAU *et al.*, 2000; GARCIA AND BASELGA, 2002 c). GARCIA AND BASELGA (2002 c) did not find correlated responses on growth traits in a line selected for litter size at weaning when two distant generation were compared using litter size at birth as a covariate. The effect of the covariate was negative as expected. The meaning of these results is that two rabbits belonging to two different generations will have the same growth performance if they are born in a litter of the same size. GARREAU and ROCHAMBEAU (2003) have estimated the genetic parameters of direct and maternal genetic effect of individual weight at weaning and at 63 days in the maternal line A1077 selected at INRA: The unfavourable genetic trend of maternal effects of weights, estimated by the REML/ BLUP methodology, is partly explained by the negative correlation between direct and maternal effect for both weaning and 63 days weights (-0,30 and -0,48, respectively). These estimates are consistent with the results obtained in a male line (LARZUL *et al.*, 2003) and in the Botucatu line using a model without any common litter effect. MOURA *et al.* (2001). In pigs, several studies have shown that selection for litter size has led to higher piglet mortality (RHYDHMER, 2000, HUBY *et al.*, 2003). Some authors stated that the uniformity in birth weight is as important as high average birth weight for piglet survival (ROEHE and

KALM, 2000; HOGBERG and RHYDMER, 2000; DAMGAARD *et al.*, 2003). These conclusions are consistent with the last surveys dealing with the homogeneity of kittens weights within litters. In their respective experiments, POIGNER *et al.* (2000) and PERRIER *et al.* (2003) have decreased the mortality of young rabbit by intra-litter homogenization of birth weights. In this context, GARREAU *et al.* (2003; 2004) have estimated the genetic parameters of the variability of birth weight and have started a divergent selection experiment for the homogeneity of birth weight using a recent method developed by SAN CRISTOBAL *et al.* (1998) incorporating a genotypic value for the mean and a genotypic value for the environmental variance.

Productive life.

Longevity has never been introduced in rabbit selection programs: it is difficult to improve through conventional breeding methods because of the low heritability of this trait and the time needed to obtain information. However, in mice, it has been clearly demonstrated that it is possible to improve reproductive life and number of parities by selection on phenotypic performances (FARID *et al.*, 2002). Some studies in rabbit population have considered the number of litters, the number of mating or the age at culling to estimate genetic parameters or compare different lines. LUKEFAHR and HAMILTON (2000) showed that Californian does had a lower longevity than New Zealand does, on the basis of age at culling (180 and 262 days, respectively), associated with a lower number of matings (4.54 and 6.09, respectively). The crossbred does (Californian x New Zealand) were at the New Zealand level (261 days and 6.12 matings). Using REML-methodology, YOUSSEF *et al.* (2000) estimated heritability values of 0.08 and 0.13 for number of litters and length of productive life, respectively. The longevity does not seem unfavourably influenced by litter size. When litter size is taken into account in the model of analysis, does with higher litter size are not more susceptible to be culled than does with lower litter size. The risk of culling largely increases for very low litter sizes (0 or 1 kit per litter, SÁNCHEZ *et al.*, 2003). Similarly, increasing litter size by selection did not increase culling rate (TUDELA *et al.*, 2003). One spreading method for analysing female longevity data is survival analysis. Applying this methodology, GARREAU *et al.* (2001) and SANCHEZ *et al.* (2003) estimated an heritability value between 0.05 and 0.24, depending on the model used for analysis. In order to confirm the efficiency of selecting on longevity applying survival analysis a selection experiment has been settled at INRA experimental farm. Energy deficit and depletion of body stores, due to milk production, could lead to a decrease of reproductive performance. Allocation of resources theory states that traits consumed environmental resources and that these resources are additively related. They can sum to no more than the total of resources an animal can obtain from the environment. Resources are allocated mainly to selected traits. This selection could act to the detriment to other traits. FORTUN-LAMOTHE (2003) demonstrated that lactation is the priority trait for a crossbred doe. Competition between foetal growth and lactation is unfavourable to foetal growth. Allocation of resources theory must be taken into account to choose the selection criteria in maternal lines.

INVENTORY OF THE SELECTED MATERNAL LINES ALL OVER THE WORLD. (Table 1)

Brazil

A multi-purpose line was selected in Brazil through simultaneous selection for litter size and growth traits (MOURA *et al.* 2001). This “Botucatu” line is still under selection. The multi-purpose index is no longer used. The selection criteria are litter size at weaning and post-weaning growth rate. An independent level selection is practised.

Egypt

V-line rabbits were imported from Spain and various selection experiments were started out. On one hand, three replicates of V-line were created: one line (Egyptian-Alexandria V) is selected for litter size at weaning (EL-RAFFA 2000); a second one (Egyptian-Moshtohor V) is selected for litter weight and live weight at 56 days, and a third one (Egyptian –APRI V) is selected for litter weight at weaning. On the other hand, two synthetic lines were started out : the Egyptian- Moshtohor Synthetic line is a cross between Sinai Gabali and V-line; the line is selected for litter weight at weaning and live weight at 56 days. The Egyptian–APRI synthetic is a cross between Baladi red and V-line; the line is selected for litter weight at weaning.

France

Two historical French selection experiments for litter size are still going on. 2066-line is selected for litter size at birth. 1077-line is selected for litter size at birth and for individual weight at 63 days (ROCHAMBEAU 1998, GARREAU and ROCHAMBEAU 2003). Two new selection experiments started up in 2003. Firstly, 1077-line was duplicated. The selection objective of the new line (1777-line) combines litter size and maternal qualities. (GARREAU and ROCHAMBEAU 2003). For the moment, there are three selection criteria: direct and maternal effects of individual weaning weight and litter size at birth. Longevity will be added soon as a fourth criterion (GARREAU *et al.* 2001). Optimum contribution selection methods maximise genetic response while constraining inbreeding by restricting the coancestry among selected parents (GRUNDY *et al.* 1998, SONESSON and MEUWISSEN 2000). These methods are used to manage 1777-line. Secondly, a divergent selection experiment was started for the homogeneity of birth weight (GARREAU *et al.* 2003; GARREAU *et al.* 2004).

Saudi Arabia

V-line rabbits were imported in 2000 and were crossed with one desert Saudi breed (Gabali). There were some evidences that V-line rabbits and their crosses could produce efficiently under hot climatic conditions (KHALIL *et al.* 2002, MEHAIA *et al.* 2002, AL-SOBAYIL AND KHALIL 2002). Two lines were initiated: one replicate of the V line and a synthetic between Gabali and V-line rabbits, both selected for litter weight at weaning and individual weight at 74 d.

Spain

Two long term selection experiments are carried out in Spain. GARCIA and BASELGA (2002 a, b, c) have analysed the response to selection. A review of the results is in the

paper presented in this Congress by BASELGA (2004), that also inform about two more recent lines founded by applying very high intensities of selection for the traits of interest. The foundation of H-line was based on the detection of hyperprolific does. H-line is now selected for litter size at birth. The same alternative was applied to create the new B-line for which the criteria of screening in the commercial farms were hyperlongevity and litter size over the mean.

Uruguay

Two lines are selected for litter size at weaning (CAPRA *et al.* 2000, GARCIA *et al.* 2000). The first one is a New Zealand White line and the second one is a duplicate of the V-line.

Comparison of genetic direct and maternal effects for various lines

The performance of a crossbred doe is the sum of the mean value of the parental lines and of the heterosis. Even if heterosis effects are of great importance, the mean value of parental lines deserves some comments. CIFRE *et al.* (1998 a and b) made a comparison of a new high prolificacy line (H-line) with V-line. The comparison was always favourable to line H (around 0.50 young rabbit) but not significant. The critical probability was around 0.06. Contrasts between H-line and V-line were not significant for first and second parity, but were very important for superior parity orders. Moreover, H-line had a higher live litter weight at birth and a higher litter weight at 21 days than V-line. The differences were mainly due to litter size. The higher prolificacy of H-line had not implied a reduction of the average weight of young rabbits. H-line was superior in individual weaning weight to V-line in agreement with its higher litter weight at 21 days, but there was no difference for time to market weight and average daily gain between the two lines. BASELGA *et al.* (2003) estimated the direct and maternal genetic effects between A, H and V-lines. Significant differences in direct genetic effects between lines were found for litter size traits. V-line had higher litter size than A-line. The differences between H-line and V-line were in favour of V-line but they were not significant. The observed differences between lines in the maternal genetic effects were small and not significant. ORENGO *et al.* (2003) studied reproductive traits between three Spanish maternal lines. Differences between direct genetic effects of A-line vs. P-line and V-line were significant for total litter weight at birth and number of alive rabbits at birth. There were also a significant difference between A-line and P-line for litter size at weaning. A-line had smaller direct genetic effects than H-line and P-line. No difference was found between maternal genetic effects. BRUN *et al.* (1998) made a comparison of V-line with 2066-line. V-line does were heavier at insemination than 2066-does. 2066-line does shed more ova (15.5 vs. 14.2), had a lower prenatal survival and the same litter size at birth and at weaning than V-line does.

Global objective

In countries where the rabbit industry has not yet reached a high level of organisation, it may not be possible to select sire and dam lines for a subsequent crossbreeding program. An alternative could be the development of a multi-purpose line, through simultaneous selection for litter size and growth traits. This alternate strategy was successfully tested in Brazil, Spain and France. MOURA *et al.* (2001) initiated the

selection of a multi-purpose line in 1992. There were four selection criteria : litter size at weaning, individual weaning weight, litter weaning weight and individual 70 days weaning. These traits were combined in an index. Estimated annual genetic trends for litter size at weaning (0.04 young rabbits per litter and per year) and litter weaning weight were positive and significant. A positive direct linear trend was observed for weaning weight, but no maternal linear trend was detected. Direct and maternal trends were favourable for time to market individual weight. *MOURA et al.* (2001) observed a more consistent response for this trait, which received a higher relative economic weight in the selection index. *GOMEZ et al.* (2000) choose two selection criteria for their multi-purpose strain: litter size at weaning and individual daily weight gain. An independent level culling selection method was used. Renewal bucks (does) were selected from the 50% (80%) best ranked dams and from the 15% (25%) fast growing young rabbits. Genetic trend in litter weight at weaning (30.9 g per litter and per year) was the result of a positive genetic response in individual weight at weaning (11 g per young rabbits and per year) and litter size at weaning (0.03 young rabbits per litter and per year). Direct response on daily gain was around 1.06 g per day, with an indirect response on individual 60 days weight (38 g per young rabbit and per year). The ability of does to raise litters has also been improved because genetic response on litter size at weaning was higher than response on litter size at birth. *SALAÜN et al* (2001) selected a Rex line on a single criterion: total litter weight at weaning per doe and per year. The heritability of the trait was low (0.06) and the genetic correlation with the total litter weight at weaning (0.98) and the litter size at weaning (0.87) were high. An annual genetic trend was observed for the selected trait (342 g), which was equal to 1.7% of the phenotypic mean or 3.22% of the phenotypic standard deviation.

CONCLUSIONS AND PROSPECTS

New results allow to initiate a novel analysis of the selection objective for maternal lines, including growth traits to overcome the reduction of weights consequence of improving litter size. Various authors stated that the uniformity in birth weight is as important as high average birth weight for pre-weaning survival. There is a significant genetic variability of the variability of birth weight and a French team have started a divergent selection experiment for the homogeneity of birth weight using a novel and innovative method. One spreading method for analysing female longevity data is survival analysis and, to confirm its efficiency a selection experiment has been settled in France. An alternative strategy was initiated in Spain with the creation of a new line from does with a high longevity. Improvement of does longevity requires research in genetics but also in nutrition, pathology and breeding. Allocation of resources theory makes up a convenient framework to analyse the doe productive life and more precisely the competition between gestation and lactation during the first parities. Spanish V-line was introduced in various countries, in one case by the way of frozen embryos. This novel technology facilitates exchange of genetic material between countries. Crossbreeding programs are in progress in order to define how to combine this material with local lines. Various countries are developing commercial rabbit lines for their national industry for a subsequent crossbreeding program. An alternative could be the development of a multi-purpose line. Later, molecular genetic tools are now available and initiate a new period

for rabbit research and rabbit genetics. Spanish and French teams put forward the hypothesis that there were major genes affecting components of litter size. A genetic map with microsatellite markers distributed every 10 to 20 cM along the genome will be available soon (CHANTRY-DARMONT et al. 2004). Simultaneously, the corresponding cytogenetic map will be established in order to provide the chromosomal position of all the genetic markers. The next objectives are to localise loci of genes of interest, to study candidate genes, identified in other species like mice, pig or sheep and to elucidate the molecular nature of a few already proven major genes.

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TABLE 1 : INVENTORY OF THE ON GOING SELECTION EXPERIMENTS OF MATERNAL LINES

Name of the line	Origin	Objective	Criteria	Bucks + does	Nb generations
Saudi-1	V line	Milk yield	Litter weaning weight + 74 d weight	10 and 60	6 generations
Saudi-2	Saudi Gabali*V line	Milk yield	Litter weaning weight + 74 d weight	10 and 50	5 generations
Egyptian-Alexandria V	V line	Litter size	Litter size at weaning	45 and 130	6 generations
Egyptian-Moshtohor V	V line	Litter weight	Litter weight + 56 d weight	35 and 120	1 generation
Egyptian-Moshtohor synth.	Sinai Gabali * V-line	Litter weight	Litter weight + 56 d weight	13 and 50	1 generation
Egyptian-APRI V	V line	Litter weight	Weaning litter weight	12 and 50	4 generations
Egyptian-APRI synthetic	Baladi red * V line	Litter weight	Weaning litter weight	15 and 50	3 generations
Celeste	NZW	Litter size	Litter size at weaning	20 and 120	3 generations
Uruguay V	V-line	Litter size	Litter size at weaning	25 and 120	4 generations
Botucatu	Norfolk line	Global	Litter size at weaning + daily gain	20 and 110	1992
A-line	NZW	Litter size	Litter size at weaning	25 and 125	33 generations
V-line	4 lines	Litter size	Litter size at weaning	25 and 125	30 generations
H-line	Hyperprolific does *V-Line	Litter size	Litter size at birth	25 and 125	11 generations
B-line	High longevity	Litter size	Litter size at weaning	25 and 125	1 generation
P-line	Crossbred	Litter size	Litter size at weaning	32 and 146	
1077-line	NZW	Litter size	Birth litter size + at 63 d. weight	33 and 121	34
1777-line	1077-line	Maternal quality	Weaning weight + birth litter size	variable and 120	2 generations
2066-line	Great Russian *Californian	Litter size	Birth litter size	27 and 81	34 generations
GD-24 line	GD-24 line	Homogeneity of birth weight	Divergent selection for variability of birth weight	2 *(5 and 55)	2 generations