

GENETICS OF THE RABBIT FOR MEAT PRODUCTION : WHAT'S NEW SINCE THE WORLD RABBIT CONGRESS HELD IN BUDAPEST IN 1988? ¹ A REVIEW.

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ABSTRACT : The purpose of this paper is to review some new results about genetics of the rabbit for meat production. We examine 4 key issues : (i) domestication of the rabbit took place few hundred years ago; European Community has just approved a program of characterisation and evaluation of genetic resources. (ii) Selection for litter size is effective, as selection for post weaning growth; genetic progress are around 0.05-0.10 rabbit per litter and per generation, and 25-40 g. of slaughter weight per generation. (iii) Selection of

strains and crossbreeding between these strains could increase the litter weight at slaughter age of more than 40% in relation to the production of a pure breed. Evolution of technical results of French rabbit farms are consistent with these estimations. (iv) Remarkable progress have recently been made in molecular analysis of the existing genetic variation within animal species. The priority is the development of a low-resolution map for the rabbit.

RESUME : *Génétique du lapin de chair : Quoi de neuf depuis le Congrès Mondial organisé à Budapest en 1988 ? Une revue.* Cet article synthétise quelques nouveaux aspects de la génétique du lapin élevé pour la production de viande. Plusieurs idées émergent de cette compilation: (i) la domestication de cette espèce ne date que de quelques centaines d'années; la Communauté Européenne finance actuellement un projet de caractérisation et d'évaluation des ressources génétiques. (ii) La sélection est une technique efficace pour améliorer la taille de la portée ou la croissance post sevrage; les progrès génétiques par génération sont respectivement de 0,05-0,10

lapereau par portée et de 25-40g pour le poids à l'abattage. (iii) La sélection de souches puis le croisement entre ces souches provoquent un accroissement du poids total de la portée à l'abattage de plus de 40% par rapport à la productivité de la race pure non sélectionnée. L'évolution des résultats français de gestion technique sont cohérents avec ces estimations. (vi) La génétique moléculaire a fait des progrès remarquables ces dernières années dans l'analyse de la variabilité génétique des espèces d'animaux domestiques. Pour le lapin la priorité est maintenant la réalisation d'une carte génétique à faible résolution.

INTRODUCTION

Rabbit is bred for meat, wool and fur. Nine years ago, ROCHAMBEAU (1988) has reviewed the available literature about genetics. In the present paper, we lay emphasise on some new aspects; we examine some genetic problems related to meat production. Firstly, we analyse some parts of the genetic history of the rabbit. Secondly, we underline recent results about genetic variability for economic traits. Next, we provide an assessment of genetic improvement programs. Finally, we discuss the possible contribution of molecular genetic.

GENETIC AND HISTORICAL APPROACH OF DOMESTICATION

Rabbit has two interesting characteristics : on the one hand, wild populations still exhibit large genetic variability; on the other hand, this species is originally domesticated in Western Europe. The hypothesis of southern Spain as the origin area for rabbits is well known. Data on mitochondrial polymorphism show the existence of two maternal lineages, geographically well separated (MONNEROT *et al.*, 1994). Lineage A is described in Andalusia and Estremadur while lineage B is observed in Northern Spain, France, England, Australia and Kerguelen. Their limits in Iberian Peninsula have to be specified. Up now all domestic

breeds belong to the B lineage (MONNEROT *et al.*, 1996). Immunoglobulin diversity data and protein polymorphism highlight two genetic groups that strictly coincide with the A and B maternal lineages. Properties of these two groups are very characteristic and suggestive of two subspecies. The genetic organisation of B animals is characterised by a large geographical distribution and by the connection with domestic breeds. For nuclear genes, domestication does not lead to any reduction of genetic variability. This is consistent with the large morphological and colour diversity of the numerous breeds catalogued in Europe.

Till the end of Antiquity, the distribution of the species are tightly linked to those of climate and vegetation. Rabbits are found in the Iberian Peninsula and in the south part of France. They do not cross the Loire river (CALLOU *et al.*, 1996). During the Roman conquest, man could have transfer the species in other area but in fact the distribution remain constant. From the beginning of the Middle Age, man is the principal agent of dispersion. The species overrun Northern Europe. However, the animal is not still domestic. Rabbit are kept in warren. Old animal production books explain this original system of breeding. DESAIVE (1842) present two systems. In the first one, rabbit are bred in some large paddocks, closed with walls or wood fences. Rabbit can found trees and aromatic plants. Haystacks are dispatched here and there under wood shelter. Holes are dug. Rabbits are caught with net.

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Male rabbit could be gelded, to prevent fights between bucks. In the second one, rabbits are bred in wooden hutches. This late system is the ancestor of all the modern ones.

After this rapid historical review, there are two essential points. Domestication of the rabbit took place few hundred years ago. This is a very short period in relation to the same event in other species like pig. Original genetic resources can be found in wild populations. Subsequently, local populations do not have enough time to adapt themselves to specific breeding conditions. If hyperprolific breeds of pig have been discovered in China, we have only a very small probability to discover such populations all over the world. In relation to the history of the rabbit, the main area of interest is to find local populations in the Mediterranean regions. In another connection, two programs were presented last year (BOLET *et al.*, 1996). On one hand, a research network on rabbit production in the Mediterranean area, founded in 1985 and including 8 countries is working on the identification and characterisation of local populations and breeds (Egypt, Tunisia, Spain,...). On the other hand, the European Community has just approved a program for «Inventory, characterisation, evaluation conservation and utilisation of European rabbit genetic resources». Research laboratories and breeders associations from 7 countries are associated. These programs will allow to produce the first international inventory and description of rabbit genetic resources.

GENETICS OF FECUNDITY AND OF POST-WEANING GROWTH

Genetics of litter size and does fertility

BLASCO (1996) has reviewed the actual state of the art. In contrast to the knowledge presented at Budapest in 1988, some points are notable. Estimations of litter size heritability were included between 0 and 0.4. There is now a wide consensus for giving lower values, generally under 0.1. Statistical method to estimate these parameters were greatly improved; additional components could now be included. Environmental permanent effects of litter size are of the same magnitude than heritability. In the oldest values, the two components (direct heritability and environmental permanent effects) were confounded. The whole maternal effects for litter size is often smaller than 10%. On the other hand, maternal heterosis effects are usually over 10%. Nevertheless, all generalisations should be avoided as heterosis depends on the genetic distance between the breeds involved in the cross.

Genetic relation between reproductive and growth traits is affected by prolificacy. Correlation seems to be low and negative in prolific lines and moderately positive in less prolific and fast growing lines (CAMACHO and BASELGA, 1990).

ROCHAMBEAU (1988) has reported 4 selection experiments on litter size. Two of them are still carried out. BLUP Animal Model method allows to estimate genetic progress without a control line. BLASCO (1996) addresses the problem of these estimation, and the sensitivity to the value of the heritability, used as a prior parameter. As a consequence, control populations are still useful to separate genetic and environmental effects. The results of the Valencia experiment have changed a bit : from +0.05 to +0.10 rabbits per litter and per generation for line A; from +0.16 to +0.03 for line V. Our results are more constant : 0.08 in 1988 and 0.075 in 1996 for the line A1077 (table 1). It must be noticed that results of genetic progress given by ROCHAMBEAU *et al.*(1994) are overestimated. As a matter of fact, estimations of heritability used were overestimated. Another Spanish experiment, carried out in Barcelona was published last year (GOMEZ *et al.*, 1996). The genetic progress estimation is 0.11 rabbits per litter and per generation. Therefore selection for litter size is effective, and the realised genetic progress is around 0.05-0.10 rabbits per litter and per generation.

Indirect selection for litter size was a very promising prospect. The idea was to select on a correlated trait with a higher heritability, like ovulation rate. However homeostatic mechanisms match the progress obtained by selection. Experimental results and simulation studies lay the emphasis on litter size as the best selection criteria to improve litter size! Meanwhile, genetic analysis of the components of litter size remains essential for understanding the origin of the genetic progress.

What are the consequences of the selection for litter size? BLASCO (1996) discuss whether the best animal of a nucleus will produce crossbred does that will be the best in the commercial farm. He concludes that farms suffering of poor environment should first invest in improving the rearing conditions than in high genetic quality animals. In my opinion, a crossbred doe have a great capacity of adaptation and a great genetic potential is absolutely necessary to be competitive (Cf page 79).

Table 1 : Genetics progress in litter size per generation observed in different selection programs

Line in selection	Year of publication	
	1986	1996
- Valencia A	0.05	0.10
- Valencia V	0.16	0.03
- Auzeville A1077	0.08	0.075
- Auzeville A2066	-	0.125
- Barcelona	-	0.11

Genetic of post-weaning growth

For ROCHAMBEAU (1988), estimations of the heritability in individual body weight tend to increase with age. The median is below 0.20 for individual body weight at weaning and above 0.45 for data recorded after weaning. As for litter size, the use of an Animal Model combined with Restricted Maximum Likelihood estimates gives lower values. For example ESTANY *et al.* (1992) give the following numbers for direct heritability of weaning weight, slaughter weight and weight gain between weaning and slaughter for lines B and R respectively: 0.15 and 0.15; .019 and 0.15; 0.21 and 0.17.. Maternal variances are : 0.27 and 0.18; 0.14 and 0.12; 0.10 and 0.10 for the same lines. More realistic models explain the discrepancy between the estimates. MCNITT and LUKEFAHR (1996) introduce a more complicated model with direct heritability, maternal heritability, permanent maternal environment effects and permanent litter environment effects. The fourth effect is always greater than the maternal ones. After weaning, these maternal effects are insignificant. However I wonder how it is possible to estimate such a number of parameters! Biologic complexity is sometimes incompatible with statistic power.

Three selection experiments for post-weaning growth were reported by ROCHAMBEAU (1988). Since then, ESTANY *et al.*(1992) give more accurate estimation of the annual genetic progress. For the weight gain between weaning (28 days) and slaughter (77 days) data are +32 g per year for line B and +26 g for line R. ROCHAMBEAU *et al.* (1994) explore the selection done by a private breeding company. For the weight gain between 28 and 70 days, the genetic progress is 37 g, per year. These experiments were done without a control line. Thus results must be analysed with care. In another connection, LUKEFAHR *et al.* (1996), provide a description of a selection experiment with a control line. For 70 days body weight, genetic trend is around 29 g per generation. It is now well established that selection for post-weaning growth is effective in rabbit as in numerous species.

Thereafter, it is necessary to investigate some effects of this selection on other traits. PLA (1996) explores carcass composition and meat quality of rabbits selected for litter size or for growth rate. The purpose of his paper was to compare the quality of the meat and the carcass in three lines with different adult weights. The comparison was done using three different live weights at slaughtering. PLA (1996) provides a description of some differences between the lines. But it is not possible to distinguish effects of selection and variability between lines before the selection. The same criticism could be done to RAMON *et al.* (1996). They describe feed efficiency and post weaning growth rate of several Spanish selected lines. Line R is the heaviest and have the lower feed conversion ratio as expected. Line P is the lighter and have the higher feed conversion ratio. On the other

hand, line C has a growth rate higher than line V, but no difference was found on feed efficiency between the 2 lines.

The experimental design used by BLASCO *et al.*(1996) is more powerful. They fit GOMPERTZ curves to 125 rabbits, divided in 2 groups. The control comes from frozen stored embryos from 3rd and 4th generations of a rabbit line selected on growth rate. The selected comes from selected offspring of generation 10th. At commercial slaughter age (10 weeks), selected animals increased near 10% their live weight. Adult weight, estimated as the A parameter of the GOMPERTZ curve, was 10% higher in the selected group. As a consequence, the age at slaughter will be reduced, because the slaughter weight is fixed by the market. The animals will be more immature when slaughtered. Thus the carcass are expected to have a poorer carcass yield and a lower meat/bone ratio. Further analysis will investigate others GOMPERTZ curve parameters. Are lines with a high growth rate more or less precocious?

AN ASSESSMENT OF GENETIC IMPROVEMENT PROGRAMS

A few years ago, BRUN and OUHAYOUN (1990) and BRUN *et al.* (1992) have compared the A1077 line with the A9077 line. The first one is selected for litter size since 1975 and the second one is the control strain. A1077 does were crossed with the A2066 line bucks to produce crossbred does named A0067, which were bred with a terminal cross buck. From these results, it is possible to estimate progress due to selection and progress coming from heterosis (Table 2). We chose the litter weight at 79 days as a synthetic trait. These results are taken from real data by some calculation under some simple hypothesis. Hence they give only rough estimates. The genetic progress for post weaning growth and for litter size is greater than 15% and the heterosis effect is of the same magnitude.

During the 70's, pyramid networks for the achievements and promotion of genetic progress were set up in Europe. The operating principle of these

Table 2 : Comparison of some genotypes to evaluate the effects of selection and of heterosis

Genotype	Litter weight at 79 days	Index	Remark
A 9077 pure line	13.0 kg	100	Control strain
Terminal buck and A1077 doe	15.1 kg	116	Genetic progress =
Terminal buck and A2066 doe	16.1 kg	125	16%
Terminal buck and A0067 doe	19.0 kg	146	Heterosis = 21%

networks is simple : a company built up a significant amount of genetic achievement in several strains. That is the last step at the peak of the pyramid in selection ties. The number of animals from these strains are subsequently increased and crossbred within single or multiple level promotion network. A network is made up of several multiplier herds. The aim is to obtain a buck for terminal cross and a crossbred doe, which is to be introduced in commercial rearing farms. These farms are the base of the pyramid. These schemes produce important batches of homogeneously performing animals. They play an essential role in the rationalisation of rabbit breeding in intensive European breeding systems. These schemes could also present drawbacks. They used to become efficient schemes for the spread of sanitary problem. Therefore, it is important to check the quality of the animals produced. Two complementary initiatives were initiated in France in the mid 80's (ROCHAMBEAU, 1988). They are still going on, and the assessment is largely positive. Sanitary status of the breeding rabbits is improving steadily. One day young rabbit sales and the use of grandparent does in commercial farms are of great help.

In what extend do we succeed to increase the animal rate of adaptation with regard to breeders' requirements? To answer, it is necessary to take down the data relating to the technical and economic performance from a sample of commercial breeding farms. RAFEL GUARRO (1996) have reviewed such recording systems employed in rabbit management. Table 3 presents the evolution of technical and economical results in a sample of French breeding

farms between 1974 and 1995. This sample included some well-run breeding farms, but it would be possible to reach much higher standards. ROCHAMBEAU (1988) has done the same analysis for the period 1974-1986. The productivity rate per doe was stagnant between 1982 and 1986, after a period of improvement since 1974. This result was the outcome of a shortening of intervals between litters, a rise and then a stabilisation of litter size at birth, an increase in pre- and post-weaning mortality rates. Renewal rate almost doubled during this period. Finally margins on feed expenditures increased positively between 1974 and 1986, but the rate of increase has been lower than the rate of inflation since 1982.

During the period 1988-1997, two main events are essential : artificial insemination is now widely used in France and is still increasing; at the same time, batches breeding systems are steadily rising. One batch system, with 42 days between 2 consecutive inseminations is leader at the moment. However, these major changes only modify partially the French mean results : the productivity per doe and per year was increased "only" by 12% between 1986 and 1995.

The main points of the technical and economical results are : (i) a different management of the does with the increase of fertility and of the interval between 2 litters and the decrease of does renewal rate; (ii) litter size goes up steadily and mortality rates level off. As a consequence, productivity per doe rises slowly; (iii) employment rate and productivity per cage of maternity accelerate steadily; (iv) gross feed conversion rate and price of pelleted feeds fall regularly and compensate

Table 3 : Results of the French technical and economical production traits registration system "RENALAP" between 1974 and 1995

Year	1974	1983	1986	1992	1995
Nb breeding units under control	-	404	543	1101	947
Fertility rate	57%	68%	70%	73%	77%
Interval between 2 litters	69 days	48 days	49 days	51 days	52 days
Litter size at birth	7.2	7.7	7.9	8.6	9.0
Birth-weaning mortality	19%	21%	23%	19%	20%
Weaning-slaughter mortality.	8%	15%	13%	13%	12%
Nb rabbit produced/doe/year	29.0	41.1	42.6	46.0	47.8
Yearly does renewal rate	83%	141%	157%	131%	122%
Maternity Cages employment rate	85%	104%	119%	142%	149%
Nb rabbit produced / maternity cage & /year	25	43	51	65	71
Gross feed conversion rate	4.50	4.37	4.23	3.95	3.84
Price of pelleted feeds (F/kg)	0.78	1.67	1.68	1.53	1.39
Price of slaughter rabbits (F/kg alive)	5.40	12.57	13.69	11.99	10.81
"Profit" on feed costs per doe & per year corrected for inflation	536 F	648 F	774 F	603 F	592 F

the sharp decline of the price of 1 kg of alive rabbit. Profit on feed costs fall regularly when expressed per kg of live rabbit produced, but when expressed per doe and per year it remains in 1995 at a level similar to that observed in 1974 after a maximum observed in 1986 (table 3).

A second way to test the effectiveness of pyramidal schemes is to study individual production data in commercial farms. It is necessary for that to use an individual technical management (RAFEL GUARRO, 1996). Unfortunately, the number of does managed with this system in France is too small to have a confident sample. Thereafter, we must consider the grandparent does, i.e. mothers of commercial ones. The A1077 strain is selected for litter size at weaning (ROCHAMBEAU *et al.*, 1994a), and is used in a pyramid net work (ROCHAMBEAU, 1988). This strain gives the does which are crossed with A2066 bucks to produce the A0067 crossbred does. Each year we collect more than 20.000 litter data. Litter sizes at birth go up gradually from 1976 to 1985 and then level off (Fig. 1). After 1992, they rise up again. Litter size at weaning accelerate until 1979 and flatten out from 1980 to 1984. After, it accelerates steadily. After 1990, an increasing percentage of rabbits sold at birth in multiplier herds force us to consider this trait with caution. Consequently, litter sizes go up in these multiplier farms, and the annual increase is consistent with the genetic progress estimated in the selection farm.

POSSIBLE CONTRIBUTION OF MOLECULAR GENETICS TO THE RABBIT'S FUTURE

ROCHAMBEAU (1988) summarised the knowledge in rabbit molecular biology. More than 60 genetic markers were described. They were either genes producing visible effects or genes coding for enzymes. Since this review, 37 markers were located in 8 autosomes and in X chromosomes; 23 markers made up 6 linkage groups,

but 6 markers have not yet been located. Various teams had carried out some gene transfers. The technique of transferring genes via micro-injection appeared to work even in rabbits. Which gene would be considered as suitable for transferring? As a conclusion, a deeper knowledge of the rabbit genome was essential to go on.

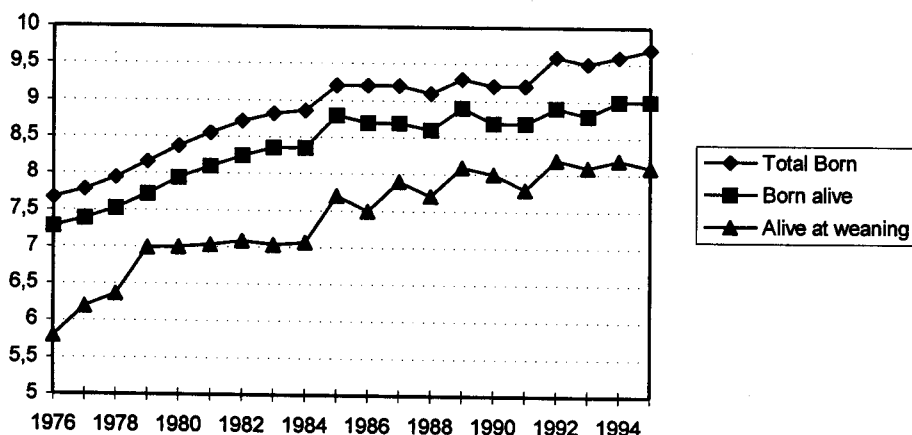
Remarkable progress has recently been made in molecular analysis of the existing genetic variation within animal species. These studies are based on the development of simple and efficient methods of polymorphism detection at the DNA level. The main results are: (i) for several already detected major genes, closely linked polymorphic marker loci have been identified, (ii) among these major genes intervening in production traits, only few have been characterised, and (iii) chromosomal regions containing previously undetected genes involved in zootechnical performances (Quantitative Trait Loci, or QTL) are now under study.

There was no co-ordinate mapping program of the rabbit, similar to those initiated in other livestock species. Consequently, no genetic map of the rabbit has been published recently. On the other hand, rabbit is widely used for physiological studies and databases contain over 1000 rabbit DNA sequences. Among them, 51 contain microsatellite sequence with a sufficient number of repetition to be polymorphic. The priority is the development of a low-resolution map. Previous result in other species have clearly shown that the efficiency of such a mapping program is increased by a large inter-laboratories collaboration. The French Research Institute INRA is now working such a project and is looking for partners.

Rabbit populations exhibit considerable phenotypic variation in growth, reproduction or fur quality. Studies in mouse or man now provide candidate genes, whose variation could explain the observed phenotypic variations. For example, we are currently testing the hypothesis that the angora mutation of rabbits is due to a defect in the FGF5 gene (MULSANT *et al.* ROCHAMBEAU, 1996).

Transgenesis is at present of poor value in selection scheme. Micro-injection procedure adds one external gene to the resident endogenous ones and does not allow to control neither the integration site nor the copy number of the transferred gene sequences. However, it enables to perform « gain of function » experiments, and for instance, it should be of use to test the direct involvement of the FGF5 gene in the angora phenotype, by transferring a functional FGF5 gene into non angora embryos.

Fig 1 : Litter sizes in the multiplier tier for A1077 does



Such obvious candidate genes will not be always available. For already identified major genes, a first mapping experiment is likely to be necessary to define more precisely the chromosomal region where they are located, and search candidate within this region. Protocols aiming at the rapid isolation of a first marker linked to the studied gene is an interesting alternative to a systematic project. In the same way, the first rabbit QTL programs could be restricted to zootechnical traits which are currently difficult to measure (for instance, disease resistance). They could be of the simplified type, a few candidate chromosomal regions being tested, in order to maintain the number of DNA typings to an acceptable level. The cost of a complete genome scan (1000-1500 individuals in large families, typed at a minimal number of 100-150 loci) can be estimated at more than 300.000 Euros.

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