

EVOLUTION OF THE GENETIC PARAMETERS OF LITTER TRAITS
IN CROSSES OF TWO SELECTED STRAINS OF RABBITS : A SYNTHESIS

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INTRODUCTION

When crossbreeding two strains knowledge of the genetic parameters allows to analyse the biological basis of the variation between crosses and particularly to understand the superiority of any one : complementarity between additive genetic effects (direct, maternal or grand-maternal) or/and heterosis (direct or maternal). These parameters also allow to predict the value of new crosses. When the strains are selected, these parameters may undergo changes, due to changes in the gene frequencies in the strains themselves. It is therefore useful, in the case of selected strains, to estimate periodically the genetic parameters of their crossbreeding.

Means and genetic parameters of litter traits in the crosses of two selected strains of rabbits were estimated in two experiments, 1970-1971 and 1979-1980 (Brun et Rouvier, 1984, 1988). These two strains, INRA A1066 and A1077, originated respectively from Californian (CA) and New-Zealand White (NZ) breeds and had been selected for litter size since 1976. They went through a multiplication system, leading to the production of a crossbred breeding doe (INRA 1067 - σ^1 1066 x ϕ 1077) with high reproductive performances. In 1985, a demultiplication tier was added and this provided the opportunity to study new crosses which appeared in the development of this new multiplication system. Besides, several studies were carried out on the biological components of litter size : number of ova shed, number of implantation sites and of live embryos (Hulot et Matheron, 1979, 1981). Therefore, it appeared useful and possible to make a synthesis about the evolution of genotypic means and genetic parameters of some litter traits over a 15 years period. The following points will be discussed : evolution of genotypic means and of genetic parameters for three litter traits : litter size at birth (born alive (BA)) and at weaning (NW), average rabbit weight at weaning (WT) ; predictive value of

size parameters on the base of what happened on the components of litter size.

EVOLUTION OF GENOTYPIC MEANS

Genotypic means in the two crossbreeding designs considered (years 1970-71 and 1979-80) are shown in table 1. Two generations were present in each experiment. Both experiments were performed in INRA experimental stations : at Toulouse-Auzeville in 1970 and at Le Magneraud in 1979 (Brun et Rouvier, 1984 ; 1988). The means reported of the 8 litter types are respectively, for experiment one and two : BA = 7.60 and 8.47 ; NW = 6.76 and 7.07 and WT = 605 g and 595 g. In the second experiment, first generation crosses were recorded for the first two parities only, the depressing effect of which is well known (Rouvier et al., 1973). Taking only the second generation into account, the means of the two experiments were respectively : BA = 7.78 and 8.89 ; NW = 6.81 and 7.60 and WT = 614g and 614 g. Within a period of 9 years, the average increase of litter size at birth was greater than at weaning (1.11 vs. 0.79). Body weight at weaning did not vary.

TABLE 1 - Estimated genotypic means for crosses between strains CA and NZ in two experiments

Year	1970-1971			1979-1980		
	BA	NW	WT	BA	NW	WT
Trait crosses *						
CA x CA	7,31	6,57	5,62	7,81	5,71	5,64
NZ x NZ	7,13	6,17	6,09	8,03	6,87	5,78
NZ x CA	7,77	7,37	5,84	8,26	6,92	5,67
CA x NZ	7,44	6,73	6,33	8,08	6,69	5,92
T x (CA x CA)	7,70	6,72	5,87	8,79	7,54	6,15
T x (NZ x NZ)	7,94	7,18	6,40	8,64	7,49	6,16
T x (NZ x CA)	7,55	6,00	6,29	9,03	7,91	5,90
T x (CA x NZ)	7,95	7,33	6,00	9,09	7,47	6,35
T x (All)	7,78	6,81	6,14	8,89	7,60	6,14

BA, NW and WT = Number of rabbits born alive, weaned and average rabbit weight at weaning

* : Sire line in given first.

In the absence of control population, it was not possible to evaluate the genetic part of this improvement, resulting from the selection carried out in the base strains since 1975 (Matheron et Rouvier, 1977). Its magnitude concorded with that of the phenotypic progress recorded on other offsprings from the same strains : NZ dams recorded either at the selection level or at the multiplication level (table 2).

TABLE 2 - Annual phenotypic progress for the New-Zealand White (NZ) dam litter traits in three environments. Mean \pm standard deviation for number born alive (BA), number weaned (NW) per litter, individual weaning weight (WT)

Trait	Tx NZ cross * in 1970-71 and 79-80 in Station	Selection experiment from 1976 to 1982 in Station	CA x NZ cross from 1976 to 1984 Multiplier farms
BA	0,08 \pm 0,04	0,13 \pm 0,06	0,17 \pm 0,02
NW	0,03 \pm 0,03	0,08 \pm 0,09	0,16 \pm 0,03
WT(g)	not calculated (*)	12 \pm 3,4	unrecorded

* : T is a terminal sire line, differing between the 2 crossbreeding experiment.

The annual genetic gains realized in the NZ strain at generation 8 were 0.14 and 0.08 rabbits at birth and at weaning respectively. This suggested a genetic basis in the evolution of the means between crossbreeding experiments and at the multiplication level. In the selection nucleus, the change in litter size was again greater at birth than at weaning, which suggested a maternal influence limiting the increase of litter size at weaning. It was not the case for the multiplication tier where BA and NW showed the same rate of increase. The relatively high increase on NW proceeded from a low initial value in 1976 (NW = 5.79) followed by a swift increase due to technical improvements in breeding procedures (Matheron et Poujardieu, 1984).

EVOLUTION OF GENETIC PARAMETERS

The evolution of genetic parameters can be assessed in two ways : firstly by comparing two subsequent estimations and secondly by testing their predictive value for crosses performed at later stages.

Parameter estimates : 1970-71 vs. 1979-80

Table 3 (Brun et Rouvier, 1988) allows a comparison of genetic parameters estimated in 1970-71 and in 1979-80. These parameters represented additive genetic effects of the strains (direct, maternal and grand-maternal, respectively g_{NZ}^I , g_{NZ}^M and $g_{NZ}^{M'}$ with $g_{CA}--g_{NZ}$) and heterotic effects (direct and maternal respectively called h^I and h^M). The positive maternal effect of the strain CA on litter size at birth remained unchanged ($g_{CA}^M=+0.36$ and $+0.37$ respectively). This effect can be attributed to the superiority of strain CA for ovulation rate. In both experiments, the pattern of h^I was the same : not significantly positive for BA but

significant for NW (10.7 % and 8.3 %), which confirmed an heterotic effect on survival rate between birth and weaning. In 1979, a positive direct effect was reported on NW, in favour of strain NZ ($g^I_{NZ}=+0.70$). Being not significant on BA, this NZ effect therefore seemed to influence survival rate after birth. This could have resulted on one hand from different selection objectives in the two strains (selection aimed at improving litter size at weaning in strain NZ but at birth in strain CA) and on the other hand, from inbreeding whose level is probably higher in strain CA, due to its smaller size. The strain difference for ^{grand-}maternal additive effect on NW changed in direction (in favour of strain NZ in 1970 but conversly in 1979) and also in magnitude ($g^{M'}_{NZ}=0.66$ and -0.22 in the 2 experiments respectively). Another change concerned the occurrence in 1979 of maternal heterosis on litter size at birth ($h^M=4$ %) and at weaning ($h^M=2.4$ %, not significant) while there was none in 1970.

TABLE 3 - Estimated genetic effects on litter traits in 2 crossbreeding experiments : 1970-72 and 1979-80

	g^I_{NZ}		g^M_{NZ}		$g^{M'}_{NZ}$		$h^I_{CA \times NZ}(\%)$		$h^M_{CA \times NZ}(\%)$	
	1970	79	70	79	70	79	70	79	70	79
Litter size at birth	0,08	<u>0,20</u>	-0,36	<u>-0,37</u>	0,20	0,03	5,3	<u>3,2</u>	0,0	4,0*
Litter size at weaning	0,12	<u>0,70*</u>	-0,98*	<u>-0,12</u>	0,66*	-0,22*	10,7*	<u>8,3*</u>	-4,2	2,4
Average rabbit weight at weaning	-1	<u>-5⁺</u>	39*	<u>13⁺</u>	-14,5	1 ⁺	3,9*	<u>1,5⁺</u>	0	0

For any additive effect, $g_{CA} = -g_{NZ}$; CA = Californien ; NZ = New-Zealand White

$g^I, g^M, g^{M'}$ = additive genetic effect resp. direct, maternal and grand-maternal

h^I, h^M = direct and maternal heterosis

* : $P < 0,05$; +: $P < 0,10$, Underlined values has been estimated over the 1st 2 parities only

Prediction of the value of later crosses

With the development of a new system of strain dissemination, through the addition of a demultiplication tier, new crosses occurred, some of them being produced simultaneously in multiplication farms. This was the case of a sample of multipliers in 1982 (Roustan et Poujardieu, 1984) and of one demultiplier in 1985 (unpublished results). This offered the opportunity to test whether intra-farm differences between crosses could be accounted for by previously estimated genetic parameters. These crosses and their values for BA and NW are shown in table 5.

Their predicted genotypic value (table 5) were expressed as deviation to the mean μ of the two pure strains (which was unknown), using Dickerson's genetic decomposition (table 4) and the 1979-80 parameters (table 3). Errors of prediction increased from 1982 to 1985 and differences of ranking of the genotypes between observed and predicted values appeared in 1985. The decrease in predictive value with time indicated that the genetic effects of the two strains continued to evolve.

TABLE 4 - Decomposition of crossbred means into DICKERSON's genetic effects for litter traits

Crosses (1)	$\mu(2)$	$g^{I}NZ$	$g^{M}NZ$	$g^{M'}NZ$	h^I	h^M
CAx[(CAxNZ)x(NZxNZ)]	1	-1/4	+1/2	1	3/4	1/2
CAxNZ	1	0	1	1	1	0
(CAxNZ)xNZ	1	1/2	1	1	1/2	0
CAx(CAxNZ)	1	-1/2	0	1	1/2	1

- (1) Sire line is given first
 (2) μ is the mean of the 2 pure strains ;
 For the other effects, see table 3.

TABLE 5 - Observed and predicted genotypic values for some crosses between some crosses between strains CA and NZ. Prediction is based on the 1979-1980 genetic parameters (table 3)

Year of production	Crosses	Observed genotypic mean(0) \pm standard deviation		Predicted genotypic value E (1)		Relative error of prediction R (2)	
		BA	NW	BA	NW	BA	NW
1982	CA[(CAxNZ)(NZxNZ)]	8,60 \pm 0,07	7,38 \pm 0,06	0,155	0,02	0,1	0,0
	CA x NZ	8,33 \pm 0,08	7,55 \pm 0,07	-0,09	0,175	0,1	0,0
	Mean \bar{O}	8,46	7,46				
1985	CA[(CAxNZ)(NZxNZ)]	9,06 \pm 0,02	8,40 \pm 0,02	0,155	0,018	3,2	6,0
	(CAxNZ) NZ	8,40 \pm 0,05	7,50 \pm 0,04	-0,115	0,267	1,1	5,0
	CA (CAxNZ)	8,80 \pm 0,10	7,40 \pm 0,09	0,40	0,212	2,3	4,3
	Mean \bar{O}	8,75	7,77				

BA - number born alive per litter
 NW - number weaned per litter

(1) E is calculated in deviation to μ which is the mean of the two pure strains CA and NZ, according to table 4. The absolute values of h^I and h^M of the 1979-81 experiment were used.

(2) R is calculated as $\frac{(O - \bar{O}) - (E - \bar{E})}{\bar{O}}$ and expressed in %

BIOLOGICAL INTERPRETATION

Can the evolution of genetic parameters of litter traits after birth be explained by what occurred to their biological components recorded before birth : number of ova shed, number of implantation sites and of live embryos at the 16th day of pregnancy ?

Evolution of the means of biological components of litter size

The means for several crosses distributed in three experiments covering a 13 years period are given in table 6. Figure 1 shows the evolution of these traits between experiments for each type of purebred dams CA and NZ. On the whole, there was an increase on each component. Of course, this increase could not be attributed to selection only. It was however possible to analyse strain differences : strain differences in ovulation rate tended to decrease : the generally accepted difference of 2 ova shed (Hulot et Matheron, 1981) fell to 1.10 in 1986-87. With regard to numbers of implantation sites and of live embryos, strain differences had entirely disappeared by 1986.

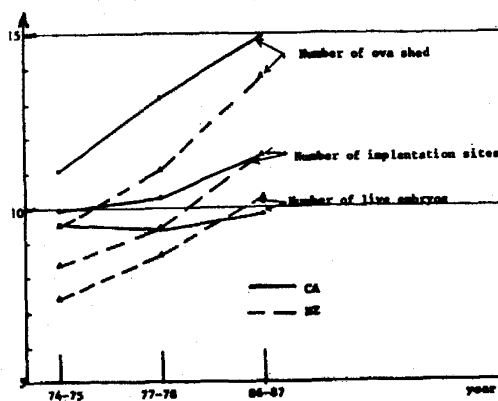
TABLE 6 - Means of the biological components of litter size for some crosses involving the strains CA and NZ in three experiments.

Year	74 - 75			77 - 78			86 - 87 (1)		
	NO	NI	NS	NO	NI	NS	NO	NI	NS
Crosses									
FB x (CA x CA)	11,07	9,93	9,53						
FB x (NZ x NZ)	9,50	8,35	7,40						
FB x (NZ x CA)	11,47	10,50	10,14						
FB x (CA x NZ)	11,50	10,32	9,66						
CA x CA				13,20	10,29	9,36	15,27	10,99	9,13
NZ x NZ				11,10	9,43	8,66	13,78	11,79	10,40
NZ x CA							14,53	11,82	10,30
CA x NZ							14,00	10,95	10,25
Significance of dam's effect.	**	**	**	**	NS	NS	*	NS	NS
Reference	Hulot et Matheron (1979)			Hulot et Matheron (1981)			unpublished		

NO, NI, NS - number of ova shed, of implantation sites and of live embryos
 The means are calculated in the population of females having at least one implantation site.
 (1) In this experiment, CA dams averaged : NO = 14,94 ; NI = 11,48 ; NS = 9,82
 and NZ dams averaged : NO = 13,83 ; NI = 11,50 ; NS = 10,33

Figure 1 -

Relative position of strains CA and NZ for the biological components of litter size in three experiments.



Evolution of the genetic parameters of litter size components

With regard to ovulation rate, considered as a dam trait, each of the three experiments allowed to estimate the sum $g_{NZ}^I + g_{NZ}^M + g_{NZ}^{M'}$, which was -0.87, -1.05 and -0.55 in the 3 experiments respectively. With regard to the numbers of implantation sites and of live embryos, considered as embryo traits, the 3 experiments (E1, E2 and E3) allowed for the following estimations :

$$\begin{array}{l}
 \text{E1} \rightarrow g_{NZ}^{M'} \text{ and } \frac{1}{2} g_{NZ}^I + g_{NZ}^M \rightarrow \left| \begin{array}{c} \frac{1}{2} g_{NZ}^I + g_{NZ}^M + g_{NZ}^{M'} \\ * \end{array} \right| \\
 \text{E2} \rightarrow \left| \begin{array}{c} * \\ g_{NZ}^I + g_{NZ}^M + g_{NZ}^{M'} \end{array} \right| \\
 \text{E3} \rightarrow g_{NZ}^I \text{ and } g_{NZ}^M + g_{NZ}^{M'} \rightarrow \left| \begin{array}{c} \frac{1}{2} g_{NZ}^I + g_{NZ}^M + g_{NZ}^{M'} \\ g_{NZ}^I + g_{NZ}^M + g_{NZ}^{M'} \end{array} \right| \text{ and } \left| \begin{array}{c} g_{NZ}^I + g_{NZ}^M + g_{NZ}^{M'} \end{array} \right|
 \end{array}$$

With the hypothesis of linear variation of the parameters, the missing values (*) and therefore g_{NZ}^I and $g_{NZ}^M + g_{NZ}^{M'}$ could be estimated for each experiment by linear intra or extrapolation. After averaging over E1 and E2, standing at an interval of only 3 years one from the other, the pattern of evolution over a 10 years period was obtained (table 7).

TABLE 7 - Estimated genetic effects on litter size at two embryonic stages

	g_{NZ}^I		$g_{NZ}^M + g_{NZ}^{M'}$	
	1974-75 + 1977-78	1986-87	1974-75 + 1977-78	1986-87
Number of implantation sites	0.35	0.83	- 0.90	- 0.43
Number of live embryos at d.16	0.70	0.76	- 1.23	0.00
Average over the 2 embryonic stages	0.52	0.75	- 1.05	- 0.21

$g^I, g^M, g^{M'}$ - additive genetic effect resp. direct, maternal and grand maternal.

Over the 2 embryonic stages, it was possible to note an average increase of g_{NZ}^I (from 0.52 to 0.75 embryos) but a decrease of the absolute value of $g_{NZ}^M + g_{NZ}^{M'}$. Thus the evolution of g_{NZ}^I on litter size before birth paralleled that observed on litter size at weaning between 1970 and 1979 (table 3). Besides, in the (E1+E2) pool, g_{NZ}^I was found suitable on embryonic survival after implantation, which was also the case in 1979 for survival between birth and weaning. This could be due to an inbreeding effect in strain CA.

The decrease of inter-strain differences in $g^M + g^{M'}$ on number of live embryos (from -1.23 to 0) seemed to have resulted from two phenomena : on one hand from a decrease in inter-strain differences in ovulation rate , on the other hand from a switch of strains for $g^M + g^{M'}$ on embryonic survival after implantation (with a negative trend of strain NZ in 1974-78 and a positive one ten years later).

The sum $g^M_{NZ} + g^{M'}_{NZ}$ represented the difference between CAxNZ and NZxCA litter sizes. The decrease of inter-strain differences in $g^M + g^{M'}$ meant that CAxNZ litter sizes became more similar to NZxCA's at the embryonic stage. Breeding does of each types would thus undergo more similar conditioning in early development which might result in a decrease of grand-maternal differences between strains on reproductive performances, such as litter size at weaning. Indeed, grand maternal differences on that trait did decrease between 1970 and 1979, $g^{M'}_{NZ}$ varying from 0.66 to -0.22. The joint evolution of [$g^{M'}$ on litter size at weaning] and [$g^M + g^{M'}$ on number of embryos] thus corroborated the hypothesis of an early determinism of the formers, which would be based on the intra-utero developmental conditions of the litter's dam. Besides, insofar as $g^{M'}$ was neither significant on number of rabbits as sites and as embryos in 1974-75 ($g^{M'}_{NZ} = -0.09$ and -0.24 resp.) or at birth in 1970-71 ($g^{M'}_{NZ} = 0.20$), it can be concluded that $g^{M'}$ effects were essentially determining viability between birth and weaning.

CONCLUSION

The mean values and the genetic parameters of litter traits in the crossing of the 2 strains of rabbits A1077 (NZ) and A1066 (CA) evolved since the constitution of the strains in 1968 : mean values increased continuously. Concerning genetic parameters, while a negative direct effect of strain CA on rabbit viability appeared, the grand-maternal advantage of the strain NZ on litter size at weaning disappeared. Consequently, these parameters only had short-term predictive values. It would be trivial to impute such changes to changes in the genetic structure of the strains through selection and inbreeding, but their biological and genetical mechanisms remained broadly unknown. However the study of biological components of litter size brought some understanding : for instance, grand-maternal effects on litter size at weaning would originate from the intra-utero developmental conditions of dams. Knowledge about the biological

determinism of litter size was still insufficient to predict the evolution of these parameters. It remained a necessity to estimate them periodically to characterize the selected strains and determine the best way to make use of them.

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The mean values and the genetic parameters of crosses between the 2 strains of rabbits CA (INRA A 1066) and NZ (A 1077), undergoing intra strain selection since 1976, had been estimated in 1970 and 1980. Eight mating types from their factorial crossing with a 3rd strain (T) as terminal sire line (male CA x female CA, CA x NZ, NZ x CA, NZ x NZ, Tx (CA x CA), Tx (CA x NZ) and so on) have been controlled for the number of rabbits born alive (BA), weaned (NW) and the average rabbit weight at weaning (WT). The averages of the 8 genotypes in the 2 experiments are respectively : BA=7.60 and 8.47 ; NW=6.76 and 7.07 and WT=605g and 595g. These differences have been discussed with reference to the phenotypic evolution of the NZ x NZ type selected in station and of the male CA x female NZ cross in farms. In the 2 experiments, the direct, maternal and grand maternal additive genetic effects of the NZ strain on NW, for instance, are respectively : $g^I = -0.12^{NS}$ and 0.70^* , $g^M = -0.98^*$ and -0.12^{NS} and $g^{MI} = 0.66^*$ and -0.22^* . The individual heterosis has remained unchanged ($h^I = 10.7^*$ and 8.3^*) while the maternal heterosis on NW has increased from 0 to 2.4^* (and to 4^* for BA). Additional crosses (1982 and 1985) have been adjusted with the 1980 parameters. In the case of selected strains, these parameters have no other predictive value than in the short term. The evolution of the litter traits parameters is compared with those of ovulation rate and embryonic survival.

EVOLUTION DES PARAMETRES GENETIQUES DES CARACTERES DE PORTEES DANS
LE CROISEMENT DE DEUX SOUCHES DE LAPINS SELECTIONNEES : UNE SYNTHESE

Les moyennes et les paramètres génétiques du croisement des 2 souches de lapins CA (INRA A 1066) et NZ (A 1077), sélectionnées intra-souche depuis 1976, ont été estimés en 1970 et en 1980. Huit types d'accouplements du croisement factoriel des ces souches, utilisées avec une troisième (T) en croisement terminal (mâle CA x femelle CA, CAxNZ, NZxCA, NZxNZ, Tx(CAxCA), Tx(CAxNZ), etc..) sont contrôlés pour le nombre de lapereaux nés vivants par portée (NV), sevrés par portée (NS) et le poids individuel moyen au sevrage (PIS). Les moyennes des 8 types génétiques sont respectivement pour les deux expériences : NV=7,60 et 8,47 ; NS=6,76 et 7,07 et PIS=605g et 595g. Ces différences sont discutées en fonction des évolutions phénotypiques de la souche NZ sélectionnée en station et du croisement mâle CA x femelle NZ contrôlé en ferme. Pour NS, par exemple les effets génétiques additifs directs, maternels et grand-maternels de la souche NZ sont respectivement dans les 2 expériences : $g^I = -0.12^{NS}$ and 0.70^* , $g^M = -0.98^*$ and -0.12^{NS} and $g^{MI} = 0.66^*$ and -0.22^* . L'hétérosisme direct reste stable ($h^I = 10,7^*$ et $8,3^*$), alors que l'hétérosisme maternel, nul en 1970, passe à $2,4^*$ en 1980 (et à 4^* sur NV). Les différences de moyennes de NV et NS pour de nouveaux croisements de ces 2 souches réalisés en 1982 et 1985 dans d'autres milieux, sont ajustées aux paramètres de 1980. Il est conclu que dans le cas de souches sélectionnées ces paramètres ont une valeur prédictive pour le court terme seulement. L'évolution des paramètres des caractères des portées est comparée à celle du taux d'ovulation et de la viabilité embryonnaire.

