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THE EFFECTS OF CROSSBREEDING AND SELECTION ON PRODUCTIVE AND REPRODUCTIVE TRAITS IN A TRIALLEL EXPERIMENT BETWEEN THREE STRAINS OF RABBITS

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Abstract

A triallel crossbreeding experiment using three INRA strains was performed : strains A1077 (named 77 below) and A1066 (named 66), originating from the New Zealand White and Californian breed respectively and selected on litter size for 13 generations and strain A9077 (named 33), an unselected control. Traits analysed were ovulation rate (NO), litter size at implantation (NI), at birth (LSB) and at weaning (LSW), rabbit weight at 30 days (W30) and at 79 days (W79), weight gain between 30 and 79 days (WG), carcass yield and carcass fatness. A total of 521 does, 975 fattened and 450 slaughtered rabbits representing 9 genetic types along with 1853 litters representing 24 genetic types were studied. Direct heterosis effects on litter size, depending on heterosis on embryo and kid survival, varied between - 1 and 6 % and were generally not significant. Therefore, single crossing generally failed to improve litter size (except with 66 dams). Conversely, double crossing through the use of crossbred dams, improved litter size dramatically, because of high maternal heterosis effects : 16, 7 and 15 % on LSW in the crosses between 66 and 77 (67), 33 and 77 (37), 33 and 66 (36) respectively. These values combined direct heterosis on ovulation rate (8 and 4%, resp. in crosses 67 and 36) and maternal heterosis on embryonic survival. Significant heterosis effects from 3 to 5 % were found on W79 and WG in crosses 67 and 63. Carcass yield exhibited low but significant heterosis effects. Carcass fatness was increased by 6 to 12 % by crossing. Strain 33 exerted favourable direct effects on embryo survival (+ 0.4 NI, LSB and LSW), growth rate (+ 1.8 g/d) and weight at 79 d (+ 80 g), unfavourable direct effects on ovulation rate and maternal effects on litter size. Strain 66 behaved just in an opposite way. Estimated on the basis of purebred dams (77 vs 33 dams) selection responses were 0.8, 1.0, 0.8 and 0.6 on N0, NI, LSB and LSW, respectively. Genetic gain on LSW therefore occurred through an increase in ovulation rate. Selection responses were magnified by crossing with strain 66 : the differences between (67 + 76) and (63 + 36) crossbred dams were more than two-fold larger than expected on a purebred basis : 1.0*, 1.1*, 0.9* and 0.7* on the respective litter size components. Such a different expression of the genetic gain in pure and in crossbreeding might be due to an effect of the genetic background (homozygous or heterozygous) on the expression of genetic variability. Selection on litter size in strain 77 apparently resulted in a decrease in growth rate, carcass yield and carcass fatness.

Key Words : Rabbits, reproduction, growth, carcass quality, crossbreeding parameters, selection response.

Introduction

Since 1976, the Station d'Amélioration Génétique des Animaux at INRA has been selecting two strains of rabbits for 13 generations : strain A1066 originates from the Californian breed and has been selected for litter size at birth. strain A1077 , originating from the New Zealand White breed has been selected for litter size at weaning in the presence of a control strain, A9077. A1066 males and A1077 females contribute to the hybrid dam A1067, used by commercial rabbit producers. After more than 10 years of selection, what is the genetic variability between these strains, both in terms of strain differences and heterosis effects? What have been the effects of selection in strain A1077, in pure and in crossbreeding ? In order to answer these questions, a crossbreeding experiment involving these 3 strains was conducted between 1987 and 1989. Analytical results concerning litter performances between birth and weaning (BRUN, 1990), biological components of litter size (BOLET et al., 1990) and growth and carcass traits (BRUN et OUHAYOUN, 1990) have already been published. This paper is an attempt to synthetise results on both productive and reproductive traits.

Materials and Methods

Experimental design. The three-step design of this experiment is described in table 1. The first step was a complete 3-strain diallel design between strains A9077 (named 33 in the below), A1066 (named 66) and A1077 (named 77). The 9 genetic types of does produced were mated in the second step with males of the 3 pure strains and produced 15 genetic types of litters. The 9 genetic types of does were studied again in the third step, mated with sires from 2 strains coming from private breeders. Performances of 1853 litters were recorded over the first three parities. During the fourth gestation, 521 females were slaugthered on day 14$\pm$1 after mating to record the number of corpora lutea, of implantation sites and of live embryos. Growth between weaning (28 days) and slaughter (79 days) was recorded in 975 kids from the 3-strain diallel design at the first and at the second step. A sample of them (450 rabbits) was slaughtered. Carcass quality was estimated by weighing perirenal fat, an indicator of carcass fatness, and other carcass components.

Traits studied. Traits reported in this study represent a sample of all traits recorded in the experiment. The reproductive traits were number of corpora lutea, implantation sites, total litter size at birth and at weaning. The growth traits were weight at 30 and 79 d, weight gain. Carcass yield and carcass fatness were the only carcass traits reported here.

Except the number of corpora lutea, all traits, including litter size, were considered as traits of the progeny. As a consequence, direct genetic effects on litter size were the effects of the genes of the embryos and kids which determine their own survival.

Statistical analyses. Data were analysed through least squares analyses of variance using the SAS GLM procedure. Least-square means of breed type of does for reproduction traits were estimated in a model including also the effects of step (1 to 3), type of mates within step and parity. Estimates of breed-types of kids for growth and carcass traits were based on a model including also the step (1 or 2) and the litter size at weaning.

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Genetical analysis. Dickerson's model (1969) was used to estimate the crossbreeding parameters of the traits studies : Direct, maternal and grand-maternal additive genetic effects (g^I, g^M and g^N respectively) along with direct and maternal heterosis (h^I and h^M). These parameters were estimated from breed-type estimates using a generalized least-square method (EISEN, 1989). In the case of growth and carcass traits, the crossbreeding parameters were estimated as weighted means of each step results (BRUN et OUHAYOUN, 1989, 1990).

Results and discussion

Breed-type estimates. Breed-type estimates for litter size at different stages are given in table 1.

TABLE 1 : L.S. MEANS OF THE 9 GENOTYPES OF DOES FOR LITTER SIZE AT DIFFERENT STAGES AND CONTRASTS ESTIMATING SELECTION RESPONSE

Genotype of does(1)	No of Corpora lutea(4)	No of implantation sites	Litter size at birth	Litter size at weaning (30 d)
33	13.0^{c}	11.0^{c}	7.8^{d}	6.9^{e}
66	14.5^{ac}	11.1^{bc}	8.5^{c}	7.2^{de}
77	13.8^{b}	12.0^{ab}	8.6^{c}	7.5^{cd}
67	15.2^{a}	13.4^{a}	9.9^{a}	8.7^{a}
76	15.3^{a}	13.1^{a}	9.9^{a}	8.8^{a}
73	12.4^{c}	10.9^{bc}	8.5^{c}	7.4^{cd}
37	12.7^{c}	11.0^{bc}	8.8^{c}	7.8^{bc}
36	13.5^{bc}	11.9^{abc}	8.7^{c}	7.9^{bc}
63	15.0^{ac}	12.5^{ab}	9.4^{b}	8.3^{b}
Overall mean	13.7	11.5	8.6	7.5
Contrasts (77−33)(2)	0.8* ± 0.35	1.0* ± 0.35	0.8* ± 0.20	0.6* ± 0.20
$\frac{1}{2}(76+67) - \frac{1}{2}(36+63)$(3)	1.0* ± 0.45	1.1* ± 0.50	0.9* ± 0.20	0.7* ± 0.20

(1) : 33,66 and 77 resp. denotes strain A9077, A1066 and A1077. In crossbreds, sire strain is given first.

(2) : This contrast estimates selection response with purebred does, whatever the type of mates. It differs from the last colum of table 5, relating to purebred litters.

(3) : This contrast estimates the correlated crossbred response to selection.

(4) : Number of corpora lutea and of implantations sites relates to the 4th parity whereas litter size at birth and at weaning relates to parities 1 to 3.

The ranking of the 9 doe genotypes was the same for ovulation rate and litter size at weaning except in does 1066 which exhibited a low pre-implantation survival and in the 73 and 37 doe genotypes. This fact shows the importance of ovulation rate in the determination of the variability of litter size between genetic types. The best performing types were the crosses between the selected strains A1066 and 1077, including the commercially disseminated INRA A1067 does. The cross between A1066 males and A9077 females (63) is also good performing. As far as dams are concerned, crossbreeding is an important source of improvement. This is not the case when only litters are crossbred ; only in the case of A1066 does, did the crossbred litters significantly perform better than the purebred ones (BRUN, 1990, BOLET et al, 1990).

Breed-type estimates for growth and carcass traits are given in table 2. Differences between strains A1066 and A1077, both selected on litter size, should be noticed, their growth characteristics did not differ but strain A1066 displayed a higher dressing percentage.

TABLE 2 : L.S. MEANS OF THE 9 GENOTYPES OF KITS FOR GROWTH AND CARCASS TRAITS (1)

Genotype of kids	Weight at 30 d. (g)	Average daily gain 30-79 d.	Weight at 79 d. (g)	Carcass. fatness % (3)	Carcass. yield %
33	600	34.0	58.4	1.48	2265
66	550	30.5	59.2	1.21	2045
77	560	31.2	57.9	1.05	2085
67	600	32.0	59.0	1.22	2170
76	580	33.4	59.5	1.33	2215
73	640	32.6	59.3	1.34	2240
37	560	32.7	58.6	1.24	2165
36	580	33.5	59.7	1.45	2225
63	620	33.6	60.1	1.38	2265
Overall mean	590	32.7	59.1	1.31	2190
Smallest significant difference	25	0.9	0.7	0.17	55

(2) : 33,66 and 77 resp. denotes strain A9077, A1066 and A1077. In crossbreds, sire strain is given first.
(3) : Carcass fatness = perirenal fat weight/carcass weight x 100.

Crossbreeding parameters. Tables 3 and 4 give these parameters for litter sizes and growth traits respectively. The effects of dam genes on litter size consist in direct effects on ovulation rate and maternal effects on viability of the embryos and kids. Concerning direct effects on ovulation rate, there was a significant variation between strains, with the following ranking of the strains : A1066 > A1077 > A9077. Then, strain A1066 lost its initial superiority because of its unfavourable maternal effect on embryonic survival or fertilization rate (BOLET et al, 1990) (0.7 embryos dead before implantation) and also on survival between birth and weaning (0.5 dead). At weaning, the strain ranking was as follows : A1077 > A1066 > A9077.

TABLE 3 : GENETIC PARAMETERS OF LITTER SIZE, CONSIDERED AS A TRAIT OF THE LITTER, AT VARIOUS STAGES BETWEEN OVULATION AND WEANING

		No of corpora lutea (1)	No of implantation sites	Litter size at birth	Litter size at weaning (30 d)
Additive	33	- 1.1*	0.8+	0.4+	0.3
Direct	66	1.2*	- 1.2*	- 0.4+	- 0.2
Effect	77	0.0	0.4	0.0	- 0.1
Additive	33	0.4	- 0.9*	- 0.8*	- 0.4*
Maternal	66	- 0.4	0.5	0.5*	0.0
Effect	77	0.1	0.4	0.3	0.4*
Additive	33	-	0.2	0.1	0.0
Grand-maternal	66	-	- 0.4	- 0.2	- 0.1
Effect	77	-	0.2	0.1	0.1
Individual	66 x 77				
Héterosis(2)	77 x 33	8*	3	5	0
	33 X 66	- 6*	- 1	1	0
		4	- 1	3	6*
Maternal	66 x 77	-	15*	15*	16*
Heterosis (2)	77 x 33	-	- 4	7*	7*
	33 x 66	-	10*	9*	15*

(1) : Unlike the other traits, the number of corpora lutea is considered as a trait of the doe.
(2) : Heterosis is expressed in percent of the parental mean.
* (+) : significantly different from zero at 5 p. 100 (10 p. 100).

Heterosis effects on ovulation rate and particularly the value of 8 % between strains A1066 and A1077 confirm previous results about the non additive genetic determinism of this trait in rabbits (HULOT et MATHERON, 1979). The existence of maternal heterosis on pre-implantation survival led to an even larger heterosis effect on the number of implantation sites and litter size at subsequent stages.

Grand-dam genetic effects on litter size were not significant. However, there was a trend to an opposition between maternal and grand-maternal effects : strain A1066 which exhibited a positive maternal effet on litter size from ovulation to birth, displayed a negative grand-maternal effect.

The additive effects of the genes of offsprings on litter size varied significantly between strains. This variability decreased from implantation to weaning. A1066 genes reduced the litter size (- 1.2 at implantation, - 0.4 at birth) while A9077 genes tended to increase it (+ O.8 at implantation, + 0.4 at birth). The effects of embryos on survival were exactly opposite to those of dams on ovulation rate, as if more ova displayed a lower viability.

Individual heterosis effects on litter size were never significant, except for litter size at weaning in the cross between strains A9077 and A1066 .

Concerning additive effects on growth traits, weight at 30 days mostly depended on maternal effects, while growth rate between 30 and 79 days mostly depended on direct effects. Strain A9077 had favourable effects on growth rate and strain A1066 unfavourable ones. A negative relationship was found between direct effects on growth rate and on slaughter yield. A significant heterosis effect was noticed in most growth and carcass traits. For instance average daily gain displayed a 3 to 5 % heterosis effect in the crosses with strain A1066. Slaughter yield was moderately, but significantly influenced by heterosis.

TABLE 4 : GENETIC PARAMETERS OF GROWTH AND CARCASS TRAITS ACCORDING TO DICKERSON'S MODEL

		Weight at 30 d. (g)	Weight at 79 d. (g)	Average daily gain 30 - 79 d	Carcass yield %	Carcass fatness % (1)
Additive	33	- 7*	80*	1.8*	- 0.8*	0.2*
Direct	66	16	- 70*	-1.7*	0.6*	- 0.05
Effect	77	- 9	- 10	- 0.1	0.2	- 0.1
Additive	33	47*	59*	0.2	0.5*	0.05
Maternal	66	- 27*	- 12	0.3	0.1	0.05
Effect	77	- 19*	- 47*	- 0.6*	- 0.6*	- 0.10
Individual	66 x 77	7*	5*	5*	1*	12*
Heterosis(2)	77 x 33	7*	2	0	1*	6
	33 x 66	4*	3*	3*	2*	6

(1) : Carcass fatness = (perirenal fat weight/carcass weight) x 100.
(2) : expressed in percent of the parental mean
* : significantly different from zero at 5 p. 100

Relationship between genetic effects on production and reproduction traits deserve some comments : the ranking of strains for maternal effects on weight at weaning was opposite to that for maternal effects on litter size.

Ranking of additive direct effects on growth ratewas similar to direct effects on litter size at birth, as if the individual growth potential was related with prenatal survival. This hypothesis is credited by the parallelism between individual heterosis effects on growth rate and on litter size at birth.

Selection response in strain A1077. The comparison between litter size of selected (A1077) and unselected does (A9077), whatever the type of mates, indicated a significant superiority of the selected strain for litter size at weaning (+ 0.6, contrast 2 in table 1). However, this genetic gain seemed to be small, compared to the expected one and even to that obtained at the 9th generation of selection (MATHERON et POUJARDIEU, 1984).

It appears even smaller and non significant (+ 0.4 rabbits) when measured in purebred litters (table 5). However, when measured in half-blood A1066 crossbred does, by comparing crossbred does from strain A1077 and crossbred does form strain A9077, the genetic gain was magnified to 0.7 weaned rabbit, indicating an additive difference of 1.4 between parents.

According to DICKERSON (1969), the total value of any pure strain, g, is the sum of three additive components, direct (g^I), maternal (g^M)) and grand-maternal (g^N) respectively. The genetic gain, $\Delta g = g_{(A1077)} - g_{(A9077)}$ could therefore be divided into 3 components, Δg^I, Δg^M and Δg^N. Table 5 indicates that selection significantly increased the maternal component of the strain value (1,4 implants, 0.8 weaned rabbits). A tendency to a decrease in direct value, controlling embryonic survival, was noticed (- 0.4 offsprings whatever the stage). The gain in maternal value on litter size resulted mainly from an increase in ovulation rate (+ 0.8 ova shed).

TABLE 5 : PARTITION OF SELECTION RESPONSE INTO ITS DIRECT, MATERNAL AND GRAND-MATERNAL COMPONENTS

	Δg^I	Δg^M	Δg^N	$\Delta g = g_{77} - g_{83} = \sum(\Delta g^k)$ (1)
No of corpora lutea	1.1* ± 0.4	- 0.3 ± 0.3	(2)	0.8* ± 0.35
No of implantation sites	- 0.4 ± 0.8	1.4* ± 0.7	0.0 ± 0.6	1.0 ± 0.60
Litter size at birth	- 0.4 ± 0.5	1.0* ± 0.4	0.0 ± 0.3	0.6 ± 0.35
Litter size at weaning (30 d)	- 0.4 ± 0.4	0.8* ± 0.4	0.1 ± 0.3	0.4 ± 0.30
Weight at 30 d (g.)	- 2 ± 12	- 66* ± 8	(2)	- 68* ± 15
Weight at 79 d (g.)	- 91* ± 25	- 106* ± 15	(2)	- 197* ± 30
Average daily gain 30-79 d	- 1.8* ± 0.4	- 0.8* ± 0.3	(2)	- 2.6* ± 0.4
Carcass yield (%)	1.0* ± 0.3	- 1.1* ± 0.2	(2)	- 0.1 ± 0.4
Carcass fatness (%)	- 0.3* ± 0.06	- 0.1* ± 0.04	(2)	- 0.4* ± 0.08

g^I, g^M, and g^N : additive effects, respectively direct, maternal and grand maternal

$\Delta g^I = g^I_{77} - g^I_{83}$ and same for Δg^M and Δg^N

(1) : For growth and carcass traits, Δg does not exactly equal $g_{77} - g_{83}$ from table 2 because the crossbreeding parameters were not calculated from table 2.

(2) : Δg^N could not be separated from Δg^M

Rabbits from selected strain A1077 were lighter at weaning, at 79 d and at the adult stage (3860 vs 4130 g) than those from unselected strain A9077. Their growth during the fattening period was also slower. Selection on litter size therefore seemed to decrease body size and growth rate. The lower carcass fatness of A1077 rabbits was in agreement with their lower ponderal maturity at 79 days (54 vs 55 % of adult weight). Both direct and maternal effects on growth rate and 79 d weight decreased by selection. Direct and maternal effects on carcass yield and carcass fatness were also significantly influenced by selection.

Conclusion

This crossbreeding experiment applied to three strains, with two of them from the same genetic pool, was fruitful. Regarding crossbreeding effects on litter size, it revealed the generally low benefit (less than 5 %) of single crossing as compared to the substantial improvement achieved through the use of crossbred does. Concerning additive direct and maternal strain effects, this experiment showed that strains A1066 and A9077 exhibited the maximum difference.

Within 13 generations, selection in strain A1077 resulted in a genetic gain of about 0.6 to 0.8 rabbits born.and 0.4 to 0.6 weaned. This response was due to an increase in the maternal component of the strain value (due to dam genes) and a trend to a decrease in the direct component (due to embryo genes). This was confirmed by the analysis of the biological components of litter size, showing an increase in ovulation rate (+ 0.8 ova shed). The apparently low selection response in strain A1077 was magnified when comparing half-blood A1066 crossbred does from either the selected or the control strain. Such a different expression of the genetic gain in pure and in crossbreeding might be due to an effect of the genetic background (homozygous vs heterozygous) on the expression of genetic variability.

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