

ANALYSIS OF REPRODUCTIVE PERFORMANCES DURING THE FORMATION OF A SYNTHETIC RABBIT STRAIN

BRUN J.M.* , BASELGA M.†

*INRA. Station d'Amélioration génétique des Animaux, BP 52627,
31326 CASTANET TOLOSAN CEDEX, France.

†Dpt. de Ciencia Animal, Universidad Politécnica de Valencia,
46071 VALENCIA, Spain.

ABSTRACT: In 1995, a synthetic rabbit strain ('2666') was formed at INRA for commercial meat purposes by crossing the INRA '2066' strain and the 'V' strain from the Polytechnical University of Valencia (Spain). The development of some reproductive traits and body weight at palpation of the '2666' does was studied from the F1 (first generation cross) to the F4 generation in comparison with the 'V' does. This development was quantified in terms of Dickerson's crossbreeding parameters. The base strains did not differ significantly for any of the studied traits, either overall or in their direct and maternal genetic value. F1 does exhibited significant individual heterosis for body weight (5.5% of the parental average), pregnancy rate (13.3%), total born (18.3%), born alive (24.4%) and weaned (21.0%) per litter born. Concerning body weight, a significant crossbred superiority over the 'V' line was retained in the F2 but not thereafter. The rate of pregnancy showed no crossbred advantage from the F2 on. Concerning litter size traits, the benefit of crossbreeding was maintained until the F4, but at a lower magnitude than in the F1. Body weight and pregnancy rate exhibited maternal heterosis, while litter size did not. Direct epistatic losses were significant for body weight, tended towards significance for pregnancy rate, but did not affect litter size. Overall, the comparison between the synthetic strain and the founders was favourable to the synthetics.

Key words: rabbit, reproduction, synthetic strain, heterosis.

INTRODUCTION

In animal breeding, synthetic or composite populations have generally been formed to combine desirable genes for commercially important traits. On the other hand, systematic crossbreeding such as single cross or 3-way crosses (utilising first-

Correspondence: J.M. Brun
E-mail: brun@germinal.toulouse.inra.fr

cross crossbred dams), are recommended in species with high reproductive rates, such as pigs or rabbits, to take full advantage of heterosis and complementarity between breeds or strains (SMITH and KING, 1964; DICKERSON, 1969; ROUVIER, 1981). In this context, inter-se matings of F1 or F2 individuals and their direct use in production is avoided because of a suspected and theoretically expected loss of heterosis in the first generations of the synthetic line.

It is classically stated that heterosis depends on intra-locus gene interactions i.e. dominance and on inter-loci gene interactions i.e. epistasis (DICKERSON, 1969; HILL, 1982; KINGHORN, 1982). Under the simple hypothesis that heterosis depends only on dominance of the direct and maternal effects, the extent of expression of heterosis in any crossbred individual, relative to that shown by first-cross individuals and first cross dams, is a linear function of the level of heterozygosity of the individuals and dams. Under this dominance model, the expectation of direct and maternal heterosis displayed by the F2 cross will be half the direct heterosis plus the total maternal heterosis, but in the subsequent inter-crossing generations is expected to be half the individual plus half the maternal heterosis. The experimental evaluations are rather scarce and conflicting (SELLIER, 1982). The F2 performance sometimes falls below the expected level and the concept of 'recombination epistatic losses' has been introduced (DICKERSON, 1969) hypothesising that favourable epistatic interactions accumulated by selection in the parental strains may be broken down by recombination when F1 individuals and dams are used for breeding.

Recently, EL-RAFFA *et al.* (2005) reported that countries with hot climates, such as Egypt and Saudi Arabia, have started a programme of forming various synthetics between exotic maternal lines and local breeds, with the aim of reaching a compromise between the performance of the exotic line and the aspect of adaptation to heat stress. The results seem very promising, but the final step, evaluation of the complete procedure, is still not complete.

The objective of this study was to evaluate and analyse the development of reproductive performance of the first 5 generations of a synthetic rabbit line. This synthetic line, identified as '2666', has been in process of formation at INRA in

Toulouse since 1995 by crossing two selected strains, one French and one Spanish (BRUN *et al.*, 1998). The present study will include all generations up to F4. The differences between the genetic types involved in these 5 generations (from F0 to F4) will be further interpreted in terms of Dickerson's model, in an attempt to estimate individual and maternal heterosis, along with epistatic losses, and to explain the development of their performance during the process of formation of the synthetics.

MATERIAL AND METHODS

Formation of the synthetic strain

The base strains were the V strain and the INRA2066 strain (subsequently referred to as '2066'). The V strain was formed in 1981 from two types of crossbreds of four strains and has been selected for litter size at weaning since 1983 at the Polytechnical University of Valencia (Spain) (ESTANY *et al.*, 1989). The 2066 strain, was formed in the 1970's based on the Russian Giant and Californian breeds and has been selected since 1976 on litter size at birth at INRA in Toulouse (France) (BRUN, 1993). The formation of the synthetics started in May 1995 when 53 pregnant does from the V strain were brought to INRA and their offspring born by hysterectomy (Table 1). The V strain was thus replicated and maintained without selection for 4 further generations in order to monitor the development of the synthetics. The strain was structured into 8 paternal origins and its size varied between 40 and 60 does. The first crossbreeding generation between the two strains took place in early 1996 (what we call generation zero or G0), producing the so-called 'F1' crossbreds. The two reciprocal F1 ($F1_V$ from V dams, and $F1_6$ from 2066 dams) were identified. F1 dams were evaluated in the presence of both parental strains between July 1996 and May 1997 (G1). The 2nd crossbreeding generation between F1 parent stock gave rise to the F2. To make the F2, the F1 breeders were crossed as follows: $F1_V$ does x $F1_V$ bucks; $F1_V$ does x $F1_6$ bucks; $F1_6$ does x $F1_6$ bucks; $F1_6$ does x $F1_V$ bucks. Subsequently, F2 breeders were evaluated between June 1997 and April 1998, in the presence of V breeders which made the connection with the previous generation. Both F3 and F4 had the same design. The V line was then cryopreserved. The 2066

strain was not included in the design after G1 because of the limited number of cages but this strain was still maintained at the ‘Centre de Sélection Femelles’ at INRA.

Breeding method

Reproduction was performed by artificial insemination (10-12 days after littering), with one insemination batch every 3 weeks and servicing the non-fertilised does in the following batch.

Statistical analysis

The traits analysed were: doe’s weight at palpation, pregnancy rate (percent of positive palpations), litter traits (total number born, number born alive and number weaned, each one evaluated per litter born).

The F0 (parentals) was defined as the purebred breeders present in G1, but not those present in G0. The data of G0 were not included in the analysis because females from both strains had had different birth conditions: the V does were born by caesarean section while the 2066 ones were not.

Table 1: Size of the genetic groups (number of does) during the formation of the synthetic line.

Generation	Strain/Cross			Breeding period
	‘V’	Crossbreds ¹	‘2066’	
G0	53		55	Oct 95-May 96
G1	45 F0	47 F1 _V / 46 F1 ₆	35 F0	Jul 96-Jun 97
G2	36	58 F2		Jun 97-Apr 98
G3	37	76 F3		May 98- Apr 99
G4	38	70 F4		Jul 99-May 00

¹F1_V, F1₆ = F1 reciprocal crosses with ‘V’ and ‘2066’ dam, respectively. The F0 was defined as the purebred does of G1 but not those of G0.

The traits were analysed using a mixed linear model with the fixed effects of the genetic type of the does (6 levels: 2066, V, F1₆, F1_v, F2, pool of F3 and F4 noted F3-4), of the physiological status of the does (combination of parity and status of lactation: lactating or not), of the year-season (3 levels at each generation, 12 levels in total) and the random effect of the does. The PROC MIXED procedure of STATISTICAL ANALYSIS SYSTEM (SAS, 1988) was utilised.

Dickerson's parameters to be estimated are μ , Δd , Δm , Hd, Hm and Rd where: μ = general mean; $\Delta d = d_6 - d_v$ (where d = direct additive genetic effect of a line); $\Delta m = m_6 - m_v$ (where m = maternal additive genetic effect of a line); Hd = direct heterosis; Hm = maternal heterosis; Rd = direct epistatic losses. In Dickerson's model, the term 'heterosis' only refers to the part of total heterosis which is linked to dominance and therefore, its expression is proportional to the heterozygosity level of the individual. These parameters were estimated by solving the equation system $G=T \times P$ expressing the genetic types' mean values as functions of these parameters; where G is the vector of estimates of the 6 genetic types (2066, V, F1₆, F1_v, F2, F3-4), P, the vector of Dickerson's parameters (μ , Δd , Hd, Δm , Hm, Rd) and T the matrix which links G to P. This equation system is expressed in Table 2 which contains the elements of the matrix T. These elements were obtained from Dickerson's model, adding 2 relationships between parameters ($d_6 + d_v = 0$ and $m_6 + m_v = 0$) in order to get a full rank system.

Table 2: Decomposition of the genetic types means following Dickerson's model.

	μ	Δd	Hd	Δm	Hm	Rd
2066	1	1	0	1	0	0
V	1	-1	0	-1	0	0
F1 ₆	1	0	1	1	0	0
F1 _v	1	0	1	-1	0	0
F2	1	0	0.5	0	1	0.5
F3-4	1	0	0.5	0	0.5	0.5

μ =general mean; $\Delta d=d_6 - d_v$ where d = direct additive genetic effect of a line; $\Delta m=m_6 - m_v$ where m = maternal additive genetic effect of a line; Hd= direct heterosis; Hm= maternal heterosis; Rd = direct epistatic losses. F3-4 is the pool of F3 and F4 types.

Maternal epistatic losses are assumed negligible. Note that F3 and F4, which have the same genetic composition, were pooled and identified as 'F3-4'.

The parameters can be calculated as: $P=T^{-1}\times G = K\times G$ where $K=T^{-1}$ and their variance-covariance matrix as: $V_p=K\times V_G\times K'$ where, V_G is the variance-covariance matrix of the estimate of P, obtained from the mixed model analysis (PROC MIXED procedure of SAS).

RESULTS

Table 3 presents the means of the 6 genetic types (see also Figure 1), the differences as compared to the V strain and the estimates of Dickerson's parameters. Strain V was chosen to visualise the development of the formation of the synthetics because, as will be explained later, there were no differences between the V and 2066 strains and the standard errors of the means of the V strain were the lowest.

Base strains and their genetic components (additive direct and maternal effects)

Base strains did not differ significantly for any of the 5 traits studied. However, does from the V strain were heavier at palpation by 101 g (2.4% of the base strains average), and tended to be more fertile (8% of the strain average). According to Dickerson's model, the difference between the lines is the sum of line differences in additive direct (Δd) and additive maternal (Δm) effects. Neither were significantly different from zero, for any of the traits.

First generation crosses and their genetic components (direct heterosis and maternal effects)

First generation crosses (F1) exhibited significant direct heterosis on does' body weight (5.5%), on pregnancy rate (13.3%), on total born (18.3%), on born alive (24.4%) and on number weaned (21.0%). Differences between both F1 reciprocal crosses (which means Δm , following Dickerson) were not significant.

Table 3: Estimates of genetic types means and of Dickerson's parameters.

	Does weight at palpation (g)	Pregnancy rate (%)	Total born	Born alive	Weaned
2066	4090±68	62.4±5.4	8.86±0.46	7.27±0.56	6.19±0.51
V	4191±26	67.7±2.1	8.66±0.17	7.72±0.21	6.73±0.19
F1 ₆	4317±64	71.4±5.1	10.34±0.42	9.40±0.52	7.76±0.48
F1 _v	4422±62	76.0±5.0	10.37±0.42	9.24±0.51	7.88±0.46
F2	4335±62	69.3±4.8	10.38±0.39	8.78±0.48	7.32±0.43
F3-4	4176±37	65.6±2.9	9.97±0.24	8.94±0.29	7.52±0.27
2066 - V	-101±72	-5.3±5.6	0.20±0.48	-0.45±0.59	-0.55±0.54
F1 - V	179±58*	6.0±4.6	1.70±0.39*	1.60±0.47*	1.08±0.43*
F2 - V	144±68*	1.6±5.2	1.73±0.42*	1.07±0.52*	0.58±0.47
F3-4 - V	-15±45	-2.1±3.5	1.31±0.28*	1.22±0.35*	0.79±0.32*
μ	4140±52	65.1±4.1	8.76±0.35	7.50±0.42	6.47±0.39
Δd	3±52	-0.3±4.1	0.12±0.35	-0.31±0.42	-0.22±0.39
Hd	230±50*	8.63±4.0*	1.60±0.33*	1.83±0.41*	1.36±0.37*
Δm	53±50	-2.3±4.0	-0.02±0.33	0.08±0.41	-0.06±0.37
Hm	318±144*	7.4±11.2	0.82±0.92	-0.32±1.13	-0.42±1.02
Rd	-475±193*	-15±15.0	-0.05±1.25	1.39±1.52	1.19±1.38

* $P < 0.05$.**Subsequent inter-crossing generations: F2 and pooled F3 and F4 (F3-4)**

The development in the subsequent generations of intercrossing seemed to depend on the trait considered. Concerning body weight at palpation, a significant crossbred superiority over the V line was maintained in the F2 but not thereafter. The rate of pregnancy showed no crossbred advantage over the V line in the F2 and F3-4. Concerning litter size, the benefit of crossbreeding was maintained until F3 and F4, but with a lower magnitude than in F1.

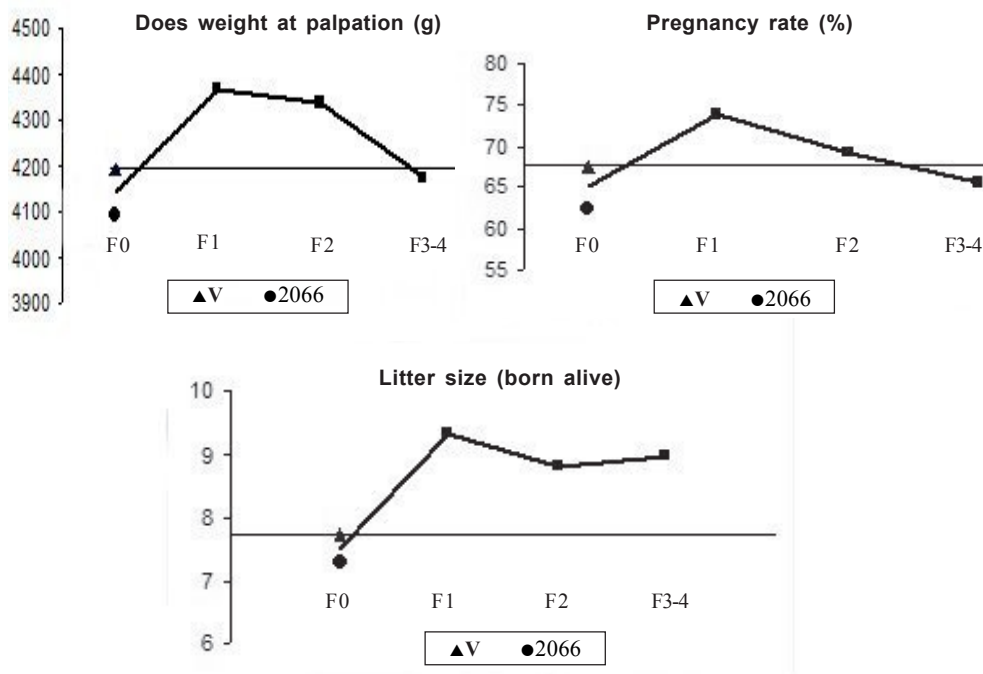


Figure 1: Performances of the synthetic strain at various generations.

Interpreting these developments in terms of Dickerson's model, body weight and pregnancy rate exhibited maternal heterosis, with the same magnitude as direct heterosis, although it was not statistically significant for pregnancy rate. This maternal heterosis explains the lower values of F3-4 does compared to F2 in those traits. Litter size did not show maternal heterosis, particularly number born alive and number weaned. Direct epistatic losses were significant for body weight, inhibiting the benefits from direct plus maternal heterosis in the F2 and in the F3-4. Pregnancy rate also showed the same, although not significant, tendencies. There were no tendencies to epistatic losses for litter sizes, particularly for number born alive and number weaned.

DISCUSSION

The present study accounted for 5 generations of the INRA2666 synthetic strain, from the F0 (parentals) to the F4 crossbreds. Partial analysis had been performed before, such as the analysis of the first generation crosses (F1), compared to the

pure breeds, either for female traits (BRUN *et al.*, 1998) or male traits (THEAU-CLÉMENT *et al.*, 1999), or the one performed after the 2nd generation cross (BRUN *et al.*, 1999).

Estimates of Dickerson's parameters

Crossing the strains V and 2066 gave rise to significant direct heterosis effects on all the traits analysed, and particularly on litter size, either at birth or at weaning. Direct heterosis on the female body weight (5.6%) is in agreement with the moderate values observed by BRUN and OUHAYOUN (1989), which were between 1.6% and 6.3% on 79 d-body weight, and AFIFI *et al.* (1994), who reported heterosis ranging between 2.7 to 9.5% for post-weaning body weights and gains, but higher than the ones obtained by KHALIL *et al.* (2005b), who observed values between 4.5 and 1.3 % for weights between 28 d and 84 d. MEDELLIN and LUKEFAHR (2001) obtained significant heterosis for weaning weight (66g) and daily gain from 28 to 70d (1.7g/d). The estimated direct heterosis on kindling rate (13.3%) was high. Other authors have studied the fertility considering other traits as the kindling interval and obtained favourable estimates for the individual heterosis, reducing the interval between 2.4 and 0.7 days (BASELGA *et al.*, 2003, between lines A and V, and A and H; ORENGO, 2003, between lines A and 'Prat', and between A and V). The high magnitude of direct heterosis on prolificacy traits (total born, born alive and weaned) is also in agreement with the values from the literature, provided that the strains which are crossed are not too closely related genetically. The heterosis estimates range between 10 and 20% in the cross between strains INRA2066 and INRA1077 (BRUN, 1993, BRUN and SALEIL, 1994), between 5.5% and 12.5% in the cross between New Zealand White and Californian breeds (NOFAL *et al.*, 1996), between 4 and 10% in the cross of line A with lines V and H (BASELGA *et al.*, 2003) and between 2.0 and 8.5% in the cross between V line and Saudi Gabali (KHALIL *et al.*, 2005a).

Maternal heterosis (7.7%) was evident for the doe weight at palpation but not for prolificacy traits. KHALIL *et al.* (2005b) found negative maternal heterosis on weights from 28 to 84 d, diminishing in importance and signification as the age increased. These results were explained as a consequence of the significant and important maternal heterosis for litter size at birth (KHALIL *et al.*, 2005a), which in a hot climate like that of Saudi Arabia could have an important negative effect on the

weaning weights and subsequent weights. Our results did not show maternal heterosis for prolificacy and the possible hybrid vigour of the crossbred dams to rear the does, without the interference of an increased litter size and a temperate climate, could be expressed as a positive maternal heterosis on the doe's weight. These heterotic effects may come partly from the genetic distance between the strains and also partly from the inbreeding accumulated in the parental strains, reproductively closed for many generations. Inbreeding depression in the base strains was elucidated by BRUN (1993) to explain the strong increase in heterosis in the cross of strains INRA2066 and INRA1077 between years 1980 and 1990. On the other hand, the absence of heterosis in the cross between lines V and H (BASELGA *et al.*, 2003) points to no inbreeding depression in these lines.

The phenotypic differences between the strains 2066 and V, at the level of the traits studied, were not obvious, except the higher body weight and the tendency to higher fertility of the V does. Moreover, for all traits, no strain differences in additive effects were found, whether individual or maternal. However, an analysis of litter size components (BRUN *et al.*, 1999) revealed that 2066 does have a higher ovulation rate than the V ones (+ 1.4 ova) and a lower prenatal (embryonic and foetal) survival (-9.4 points of percentage). The genetic differentiation between both strains also appeared at the molecular genetic level, in the study of 6 microsatellites loci (QUENEY *et al.*, 2002). Moreover, a higher number of alleles was found in strain V (4 vs 3.5), which is consistent with its larger genetic base and its shorter selection history.

Epistatic interactions were detected for doe's body weight, and, to a lesser extent, for pregnancy rate but not on litter size. KHALIL *et al.* (2005b) did not find significant direct epistatic losses on weaning and post-weaning weights and the same result was obtained by KHALIL *et al.* (2005a) for litter size traits. Our knowledge on epistatic interactions in animals is limited. There are a few reports in mice (MORTON, 1970, KINGHORN, 1982) and poultry (SHERIDAN, 1981). After the review of JAKUBEC and NITTER (1986) in sheep, a few studies reported small (favourable or unfavourable) epistatic effects for growth traits while several authors found large and negative recombination effects for female reproductive performance.

Development of the traits during the formation of the synthetic strain

Our study revealed different patterns, depending on the trait, for the development of the traits' mean during the formation of the synthetic strain. In the F₂, the mean performance varied between that of the F₁ and the average of F₁ and mid-parents. In the last crossbreeding generations studied (the pool of F₃ and F₄), body weight and pregnancy rate did not exhibit crossbred superiority any longer, while litter size retained a higher proportion of the maximum crossbred performance than that expressed in the F₁. Although synthetic strains have been often developed in animal breeding, the performances have rarely been monitored by the use of a control line. SHERIDAN (1981), summarizing 4 independent crossbreeding studies in the laying hen, found that 'heterosis' on egg production in the F₂ (in fact the crossbred superiority over the mid-parent) were consistently below the expected level on the basis of the heterozygosity level (half the F₁): 3%, 0%, 5% and 5% in the F₂ vs 15%, 18%, 18% and 13% in the F₁. On the basis of these results and other crossbreeding results in farm animals, he concluded that "the level of residual heterosis in various secondary crossbred populations should not be predicted from the performance of the purebred and F₁ populations". Such a conclusion matches our results quite well, as far as the variety of development patterns by trait is concerned.

Practical implications

Selection companies, either in plant or animal breeding, which select strains for discontinuous crossbreeding schemes generally disadvise inter-se matings of F₁ individuals and encourage the systematic provision of breeders from the selection nucleus. Our results show that inter se matings of F₁ individuals may lead to good performing F₂ animals. Nevertheless, F₁ individuals make maximum benefit from heterosis and from the gains achieved by selection in the selection nucleus.

CONCLUSIONS

Individual heterosis (in Dickerson's sense, i.e. the part due to dominance) was significant for all the trait studied: body weight, pregnancy rate and litter size.

Moreover, body weight and pregnancy rate exhibited maternal heterosis (linked to dominance). Direct epistasis was significant for body weight, tended towards significance for pregnancy rate, but did not affect litter size. The presence of epistasis makes it impossible to predict the crossbred superiority retained in advanced generations of crossbreeding from the performances observed in the F1 and F2 generations.

Focusing on the final results of the synthetic strain and the studied traits, the strain keeps performances similar to the V strain in weight of the does and pregnancy rate but significantly better for litter size traits. Thus, the use of similarly performing, but genetically different strains, is revealed as a successful way of producing superior strains.

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