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Original article

Analysis of reproductive traits in crosses among maternal lines of rabbits

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Abstract — A crossbreeding experiment, between three maternal lines of rabbits, was carried out to estimate the effects of the crosses on reproductive traits. The experiment was designed as a complete diallel cross involving the lines, A, V and H, selected for litter size. A total of 1190 does, distributed between the nine types originating from the diallel cross, and born, reared and bred on the same commercial farm, were controlled. The recorded traits were the total number of young born, the number of born alive and the number of stillborn per litter (3759 records), and the interval between kindlings (2505 records). A repeatability animal model was used first to obtain the REML estimates of the components of variance. This was followed by a generalised least squares analysis and the estimates of the type of doe effects were obtained. Finally the differences among the lines within direct and maternal effects, and the corresponding values of the individual heterosis were estimated. Important differences in the direct effects were found between lines V and A. All the maternal effects were not significant. Favourable heterosis (4–10%) was found for prolificacy traits in the crosses of line A with lines V and H, being the heterosis, very dependent on the performance and history of the lines involved.

reproduction / crosses / maternal / lines / rabbits

Résumé — Analyse de caractères de reproduction par le croisement de souches maternelles de lapin. Une expérience de croisements de trois souches maternelles de lapins a été menée pour estimer les effets des croisements sur les caractères de reproduction. L'expérience a été construite sur un schéma diallèle complet des souches A, V et H sélectionnées pour la taille de la portée par le département de Science Animale de l'Université Polytechnique de Valence en Espagne. Au total 1190 lapines nées et élevées dans la même ferme de production et réparties dans les neuf types génétiques ont été contrôlées. Les caractères mesurés ont été le nombre total de lapereaux nés, nés vivants et mort nés (3759 données), et l'intervalle entre portées (2505 données). Un modèle animal avec répétabilité a été utilisé

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dans un premier temps pour l'estimation des composantes de la variance par REML. Cela a été suivi d'une analyse GLM pour l'estimation des effets de chaque type génétique. Finalement les différences entre souches au regard des effets directs et maternels et les effets d'hétérosis en ont été déduits. Des différences importantes d'effets directs ont été trouvées entre les souches A et V. Tous les effets maternels n'étaient pas significatifs. Une hétérosis favorable (4–10 %) a été trouvée pour les caractères de prolificité entre les croisements de la souche A avec les souches V et H, cette hétérosis paraissant très dépendante des performances et de l'histoire des souches impliquées.

reproduction / croisements / lignées maternelles / lapin

1. INTRODUCTION

Intensive meat production in rabbits is based on a three way crossbreeding scheme. A first cross involves two maternal lines generating the crossbred does, which are used as females for production in commercial farms. A second cross consists of mating males of a third line, commonly selected for growth rate or weight at a given age, to the crossbred does in order to produce the rabbits to be slaughtered for meat. In this context the development of maternal lines is a crucial activity of the companies and public institutions devoted to the genetic improvement of meat rabbit production. These lines are commonly selected for litter size traits, as litter size at birth or at weaning, following within line methods of selection [2, 18, 22]. The aim of the cross between the maternal lines is to take advantage of the expected positive heterosis in the reproductive traits, the eventual complementarity among the lines and the dissipation of the inbreeding accumulated within the lines. Because the usual methods are based on within line selection, as opposed to reciprocal-recurrent selection, direct performance of the crossbred does is improved. Furthermore, it is expected that the initial heterosis expressed in the cross will be maintained along the generations of selection and that the genetic progress obtained selecting the maternal lines will be capitalised on top of the heterosis [16, 19, 23] and expressed in the crossbred does. In this sense, a very important point is to check if the heterosis is actually maintained. This is done from time to time in the French programme of rabbit breeding [20]. In Spain, the Department of Animal Science started a programme of development of meat rabbit lines at the end of the nineteen seventies. Currently, the programme has three maternal lines, called, A, H and V, that are being selected for litter size. Lines A and V are two relatively old maternal lines. Line H is a relatively recent line that was founded following a criterion of hyperprolificacy.

The aim of this work was to estimate the crossbreeding effects in the cross of the previously cited lines for reproductive traits, trying to relate the results with the performances of the lines themselves and the peculiarities of their foundation.

2. MATERIALS AND METHODS

A complete diallel cross was carried out involving three rabbit maternal lines, A, V and H, selected for litter size. Line A has been selected for litter size at weaning since 1980; the animals are evaluated using a family index [1]. Line V has been selected for the same trait since 1982 based on BLUP under a repeatability animal model [8]. Line H has been selected for number born alive per litter using the same procedure of evaluation as that used in line V. The foundation of line H was done following a criterion of hyperprolificacy [5].

The experiment, carried out on a commercial farm, near Valencia, involved 1190 does, all of which were born on the commercial farm and distributed among the nine types as shown in Table I. The does were inseminated with pooled semen of bucks from line R, and were selected for post-weaning daily gain [9]. The age of the does at first insemination was 17 weeks, and 11 days after kindling the does were again inseminated. The recorded traits were the total number of young born, number born alive, number of still born per litter and interval between kindlings. A total of 3759 parities were recorded (Tab. I).

The model used in the analysis of the litter size traits was:

$$Y_{ijkl} = D_i + S_j + E_k + a_l + p_l + e_{ijkl}$$

where Y_{ijkl} is one observation of the trait being analysed;

D_i is ith type of doe (nine levels, three pure-bred and six crossbred);

S_j is jth year season (one year season every three months: 10 levels);

E_k is kth physiological state of the doe (five levels depending on the parity order and lactation state at the moment of insemination: 1 for nulliparous, 2 (3) for primiparous lactating (no lactating), 4 (5) for multiparous lactating (no lactating) does;

a_l (p_l) is the additive value (permanent no additive value) of the lth doe at which the observation corresponds. It is a random effect;

and e_{ijkl} is the error term of the model.

To analyse the kindling interval the parity order (8 levels) was used instead of the physiological state of the doe.

First, the variance components of the random effects were estimated by REML, using the VCE software [15]. The REML estimates of the variance components were used to solve the corresponding mixed models by generalised least squares using the PEST package [14]. To estimate the estimable crossbreeding genetic parameters of the lines, the solutions obtained for D_i, represented as the vector $\hat{d}$ and their matrix of estimated variance-covariance errors, C^{ii}, were used. As we will see, the estimable parameters are the differences between direct genetic effects of the lines, differences between maternal genetic effects of the lines and individual heterosis between the lines [6]. We can suppose, without losing generality that the solution for D_5 is zero and, consequently, the interpretation of $\hat{d}$ in terms of the genetic parameters of the crosses is given in Table II, where the combination of parameters that explain the effects of the different types of does are the differences between direct and maternal effects, and the individual heterosis between lines. Thus, we have seven combined parameters to estimate, that we call vector x. It is clear that,

Table I. Distribution of the animals by line and type of cross.

Parental line[1]		Cross-breeding scheme		
Sire	Dam		Type of Doe	
A	A	AA[2]	AV	AH
80	129	112 (338)[3]	163 (573)	149 (468)
V	V	VA	VV	VH
79	131	123 (381)	147 (491)	129 (393)
H	H	HA	HV	HH
79	123	119 (386)	139 (440)	109 (289)

[1] Number of sires and dams is specified; [2] sire line is given first; [3] for each type of doe, the number of does (number of parities).

Table II. Type of does (Doe), line of the parents (Sire, Dam) and interpretation of the estimable functions (EST), as a function of the genetic parameters of the crosses[1].

Doe	Sire	Dam	EST	d_A-d_V	d_H-d_V	m_A-m_V	m_H-m_V	h_{AV}	h_{AH}	h_{VH}
1	A	A	D_1-D_5	1	0	1	0	0	0	0
2	A	V	D_2-D_5	0.5	0	0	0	1	0	0
3	A	H	D_3-D_5	0.5	0.5	0	1	0	1	0
4	V	A	D_4-D_5	0.5	0	1	0	1	0	0
5	V	V	D_5-D_5	0	0	0	0	0	0	0
6	V	H	D_6-D_5	0	0.5	0	1	0	0	1
7	H	A	D_7-D_5	0.5	0.5	1	0	0	1	0
8	H	V	D_8-D_5	0	0.5	0	0	0	0	1
9	H	H	D_9-D_5	0	1	0	1	0	0	0

[1] d_I: direct genetic effect of line I; m_I: maternal genetic effect of line I; h_{IJ}: heterosis effect between lines I and J.

$x' = \{d_A - d_V \quad d_H - d_V \quad m_A - m_V \quad m_H - m_V \quad h_{AV} \quad h_{AH} \quad h_{VH}\}$,

and x explains $\hat{d}$ through the following model:

$$\hat{d} = X.x + e$$

where X is the 9 × 7 matrix relating the solution of the type of doe effects to the combined crossbreeding parameters of crossbreeding (Tab. II). Vector x has seven elements and remembering that C^{ii} is the variance-covariance matrix of $\hat{d}$, the generalised least squares solution for x, that we call $\hat{x}$ will be unique and is equal to,

$$\hat{x} = (X'(C^{ii})^{-}X)^{-1}X'(C^{ii})^{-}\hat{d}$$

where $(X'(C^{ii})^{-}X)^{-1}$ is the variance-covariance matrix of $\hat{x}$, needed to test the significance of the components of x.

3. RESULTS AND DISCUSSION

A general picture of the size of the experiment, the crude overall means, standard deviations and range of variation of the recorded traits are shown in Table III. It is remarkable, from a productive point of view, that such a high average prolificacy was obtained, despite that the three groups of does are pure line does and that approximately one third of the records come from first parities. Higher values were obtained by Perrier et al. [21], lower values were obtained by García and Baselga [10] and even lower ones by Lukefahr and Hamilton [17], Garreau et al. [12] and Gómez et al. [13].

The REML estimates of the ratios between the variance components of the models to the phenotypic variance are given in Table IV. We define h^2 as the ratio between the additive and phenotypic variances but extended to the different lines and crosses involved in the diallele cross. The same meaning is attached to p^2, the ratio between permanent no additive effects and phenotypic variances. Similar estimates were obtained by Lukefahr and Hamilton [17] from combined purebred and crossbred data; only the h^2 estimate for total litter size at birth was higher. However, these parameters are commonly estimated within the population and the values obtained for line V were similar to the estimates reported in Table IV, except for the total litter size at birth that had estimates a little higher for h^2 and p^2 [10].The estimates in line A were, however, a little higher [11]. The estimated values in other populations are also

Table III. Mean, standard deviation (SD) and extreme values for the recorded traits.

Trait	N	Mean	SD	Minimum	Maximum
Total born	3759	10.45	3.08	1	23
Born alive	3759	9.64	3.64	0	23
Stillborn	3759	0.81	2.13	0	18
KI	2505	58.1	16.4	37	147

KI: kindling interval.

Table IV. Data on estimated variance components.

Trait	h^2	p^2
Total born	0.056 ± 0.016	0.090 ± 0.017
Born alive	0.065 ± 0.017	0.085 ± 0.018
Stillborn	0.070 ± 0.017	0.060 ± 0.018
KI	0.078 ± 0.019	0.008 ± 0.021

KI: kindling interval, h^2: heritability, p^2: ratio of variance of non-additive permanent effects to phenotypic variance.

similar with heritabilities ranging between 0.00 and 0.15 [12, 13, 17].

3.1. Direct and maternal genetic effects

Significant differences in direct genetic effects between lines were found for total litter size, number born alive and kindling interval (Tab. V), but not for mortality at birth. When significant differences exist, they favoured line V, compared to line A, with important magnitude of differences. Thus, line V showed more than 1.2 young at birth than line A and around an 8 day lower interval between kindlings. Line H did not show significant differences with lines V and A.

The observed differences between lines in the maternal genetic effects were small and not significant (Tab. V). This means that the total differences between the lines, adding the direct and the maternal genetic effects, were mainly due to the direct genetic effects that in general point to the superiority of line V relative to line A. Cifre et al. [5] in a large sized experiment comparing lines H, V and the A × V cross, found that line H was superior to the others in litter size traits and not different in kindling interval.

3.2. Individual heterosis

The results are shown in Table V. It can be seen that for the traits number stillborn and kindling interval there are small, favourable and significant values of individual heterosis, only between lines A and H. The picture for the other traits is very clear, line A showed significant individual heterosis with lines V and H in both prolificacy traits, total born and born alive per litter. The heterosis estimates range between 0.45 and 0.98 young per litter (4 and 10%). No significant heterosis, for all traits, were detected between lines V and H. Two explanations can be envisaged for this result. The first takes into consideration the fact that line H was founded by a procedure based on hyperprolificacy, selecting on

Table V. Estimable functions between direct genetic effects (d_A, d_V, d_H), maternal genetic effects (m_A, m_V, m_H) and individual heterosis (h_{AV}, h_{AH}, h_{VH}).

Trait	Total born	Born alive	Stillborn	KI[1]
d_A-d_V	–1.23 ± 0.38*	–1.39 ± 0.44*	0.15 ± 0.27	7.37 ± 2.28*
d_H-d_V	–0.62 ± 0.38	–0.87 ± 0.46	0.25 ± 0.28	0.81 ± 2.39
m_A-m_V	0.01 ± 0.23	–0.04 ± 0.26	0.06 ± 0.16	–0.80 ± 1.37
m_H-m_V	0.11 ± 0.23	–0.04 ± 0.27	0.14 ± 0.16	–0.15 ± 1.39
h_{AV}	0.48 ± 0.18*	0.55 ± 0.21*	–0.07 ± 0.13	–1.59 ± 1.07
h_{AH}	0.69 ± 0.19*	0.98 ± 0.22*	–0.28 ± 0.13*	–2.41 ± 1.16
h_{VH}	0.17 ± 0.18	0.12 ± 0.22	0.05 ± 0.13	1.65 ± 1.11

[1] KI: kindling interval; *: difference significant at $\alpha = 0.05$.

commercial farms [5] that could be highly influenced by line V and by the fact that the first batch of hyperprolific does was crossed to bucks of line V. This means that the lines V and H are genetically close and the expected heterosis should be low. The second explanation considers that V and H lines, both have a very high prolificacy, higher than line A, and consequently low differences in the frequencies of the genes affecting prolificacy and then low heterosis, as suggested by the theory of dominance for heterosis, could be expected [7]. The results obtained by Minvielle et al. [19] in quails were, however, contrary to this expectation, because the heterosis did not diminish with the progress of the selection programme. Another result contrary to the second explanation was obtained by García and Baselga [10, 11]. These authors analysed the response to selection in lines A and V, showing that the response resulted from a modification of different components of litter size, depending on the line. In line A, litter size was improved increasing the survival rate of the embryos after implantation. In line V, the improvement in litter size was due to an increase in ovulation rate without modifying prenatal survival. In this situation the difference of gene frequencies between lines A and V for the different components of litter size could not necessarily diminish and consequently the heterosis could be maintained or increased. Then, the closeness between lines V and H seems the most likely explanation for the absence of heterosis between them. In France, since the nineteen seventies INRA has been selecting two maternal lines for litter size traits. These lines named INRA 2066 and INRA 1077 are crossed to obtain the crossbred doe 1067. For the cross of these lines, Brun and Saleil [3] have estimated heterosis of 15.2%, 20.1% and 6.7% for the traits total litter size, born alive and number of weaned young. These figures are important, despite the long number of generations of selection followed in these lines. Nofal et al. [20] give values of 12.5%, 10.0% and 5.5% of heterosis for the same traits previously cited for the cross between New Zealand White and Californian. The heterosis between line V and INRA 2066 for the traits total litter size and number born alive has been studied by Brun et al. [4] reporting values of 13.6% and 20.7% for these traits.

4. CONCLUSION

Significant differences in direct genetic effects have been estimated between maternal lines highly selected for litter size, but not in maternal genetic effects for traits of prolificacy and kindling interval. The estimated heterosis was very dependent of the lines involved in the cross, ranging from negligible values to relatively important and significant figures.

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