CROSSBREEDING EFFECTS ON LITTER SIZE COMPONENTS IN RABBITS

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ABSTRACT

A crossbreeding experiment between four maternal lines of rabbits was carried out to estimate the crossbreeding effects on litter size components. The experiment was designed as a complete diallel crossing involving A, V, H and LP lines, all of these lines have been selected for litter size at weaning. A total of 2025 does, from the sixteen genetic types were subjected to laparoscopy. The sixteen genetic groups were distributed in four Spanish farms but only one group was presented in all farms to connect the data (line V). The recorded traits were ovulation rate (OR), number of implanted embryos (IE), total born (TB), number born alive (NBA), embryo survival (ES), fetal survival (FS) and prenatal survival (PS). An animal model was used to estimate components of variance using a REML procedure. Contrasts to show the differences between direct genetic effects of lines, differences between maternal genetic effects of lines and individual heterosis were estimated according to Dickerson model after solving the appropriate animal model conditioned on the REML variance components. In general, relevant but no always significant differences between lines in direct genetic effects were found. Line LP presented higher direct genetic effects than the other lines, significantly different from line A. All contrasts of maternal effects were not significant except between the LP and V lines. High positive values of heterosis contrasts were found between lines A and H. The cross between lines LP and V had negative heterosis for all traits with considerable negative effects on TB and NBA (16% and 11% of the mean, respectively).

Key words: Rabbits, Maternal lines, Crossbreeding components, Ovulation rate, Litter size, Laparoscopy.

INTRODUCTION

Litter size is the most important economic trait in maternal lines of rabbits and it is important to study its components. Litter size is determined by the number of ova shed, fertilization rate, and pre- and post-implantation embryonic mortality. Prenatal mortality is around 30% in rabbits (García and Baselga, 2002; Mocé *et al.,* 2010). The observed heterosis in litter size traits in prolific mammals could be a consequence of the superiority of the crossbreds in ovulation rate or in embryo survival, or in both at the same time. Some crossbreeding studies have considered litter size as a separate trait, but few studies dealt with components of this trait. In rabbits, Hulot and Matheron (1979) and Brun *et al.* (1992) detected positive and significant heterosis for ovulation rate and prenatal survival, while, in pigs it was not observed (Bidanel *et al.,* 1990 and Galvin *et al.,* 1993) for ovulation rate. In mice, Davis and Lamberson (1991) reported that genetic group affected significantly ovulation rate and total number of foetuses, but not total number of implantations. Falconer and Roberts (1960) and Boshier (1968) performed studies to know the results of crossing inbred lines. All results supported the conclusion that ovulation rate shows little, if any, heterosis. The last author found a considerable

degree of heterosis for fetal survival. The main objective of this study was to estimate crossbreeding effects on litter size components in four Spanish maternal lines of rabbits and their crosses.

MATERIALS AND METHODS

Animals and management

A complete diallel crossing was carried out involving four maternal lines of rabbits (A, V, H and LP), selected for litter size at weaning as described previously by Ragab and Baselga (2011). The current generation of selection is 41^{th}, 37^{th}, 20^{th} and 7^{th}, respectively. Data were collected from January 2009 to October 2011. The experimental work was carried out in four Spanish farms with a total of 2260 cages available for breeding animals. The farms were located in León (farm 1, 800 does), Castellón (farm 2, 800 does), Tarragona (farm 3, 300 does) and finally the farm of Universidad Politécnica de Valencia (UPV, farm 4, 360 does). The genetic groups involved in the experiment are four lines (AA, VV, HH and LL) and twelve single crosses (AV, VA. AH, HA, AL, LA, VH, HV, VL, LV, HL and LH, the first letter refers to the sire line, and the second to the dam line, L is used to identify the LP line in the crosses). In farms 1 and 2 all the crossbreds and purebred V line animals were raised; in farm 3 females of the groups VV and HH were raised and in farm 4 VV, AA and LL animals were housed. The group VV was used in all farms to connect data between farms. In farms 1 and 2, a single band every 42 days was practiced, while in farms 3 and 4 weekly band was practiced. In all farms, the first mating of does and bucks was around 18 weeks of age. Natural mating was used in farms 3 and 4, while artificial insemination was conducted in farms 1 and 2. In farms 1and 2, does were inseminated with semen of a paternal line (0.5 ml per doe) with a prior injection of gonadotropin to induce the ovulation. The semen was collected 16 hours before insemination. Rabbits fed *ad libitum* on a standard commercial pelleted diet. Rabbits were kept under a constant photoperiod of 16: 8 h. Management was slightly different across farms.

Traits and statistical analyses

The studied traits were ovulation rate (OR; estimated as the number of corpora lutea in both ovaries), number of implanted embryos (IE; measured as the number of implantation sites), total born (TB; measured as the total number of kits born), number born alive (NBA; measured as the number of kits born alive), embryo survival (ES; estimated as IE / OR), fetal survival (FS; estimated as LS / IE), and prenatal survival (PS; estimated as LS / OR). These records were obtained from does in their third, fourth or fifth gestations that were subjected to a laparoscopy 11-12 days after mating. The surgical technique is described by Santacreu *et al.* (1990).

All traits were analysed using the following mixed model:

$$Y_{ijkl} = GFYS_i + PO_j + L_k + a_l + e_{ijkl}$$

where Y_{ijkl} is one observation of the trait being analysed; $GFYS_i$ is the fixed effect of the genetic group-farm-year-season combination (129 levels); PO_j is the parity order (3 levels (3, 4 and 5)); L_k is the effect of lactation state of the doe (2 levels: lactating does and not lactating does at mating time); a_l is the additive genetic value of the doe at which the observation corresponds, and e_{ijkl} is the residual of the model. As a first step, the variance components for this model were estimated using remlf90 program (Misztal *et al.*, 2002). Giving the previously estimated variance components, the model was solved using blupf90 program (Misztal *et al.*, 2002) to get the model estimates, as well as their (co)variance matrix and the differences (as contrasts) between all genetic groups and the VV group. From these contrasts and its variance covariance matrix, differences between direct genetic effects of the lines, differences between maternal genetic effects of the lines and individual heterosis were estimated according to the model of Dickerson (Dickerson, 1969).

RESULTS AND DISCUSSION

Means and standard deviations of the considered traits of litter size components are presented in Table 1. The mean of OR is similar to the values obtained by other authors in selection experiments for uterine capacity or OR (Ibáñez-Escriche *et al.,* 2006; Laborda *et al.,* 2011 a&b). For the other traits, we have observed larger averages.

Table 1. Descriptive statistics of the experimental data concerning litter size components.

Trait[1]	N	Mean	Minimum	Maximum	SD
OR, ovum	2024	15.30	6.00	30.00	2.79
IE, embryo	2024	13.28	1.00	27.00	3.11
TB, kit	1856	11.03	1.00	22.00	3.32
NBA, kit	1856	10.54	0.00	19.00	3.23
ES, %	2024	0.87	0.06	1.00	0.16
FS, %	1856	0.84	0.11	1.00	0.18
PS, %	1856	0.73	0.56	1.00	0.21

[1] OR=ovulation rate; IE=implanted embryos; TB=total born; NBA=number born alive; ES = embryonic survival; FS = fetal survival; PS= prenatal survival

Differences between performances of all genetic groups and VV animals could be observed in Table 2. It is shown that the range in differences was 2.82 ova for OR, 2.12 embryos for IE, 2.99 kits for TB, 3.28 kits for NBA, 12.28% for SE, 13.85% for FS and 10.52% for PS. These figures show that the observed differences between genetic groups are important. For TB and NBA, the differences between any purebred and the line V were not significant for any trait except contrast for NBA between A and V lines was in favour of the line V. LP line showed higher values than the V line. A line showed the lowest prolificacy, 1.15, 1.68 and 1.32 less kits than V, LP and H lines for TB and 1.94, 2.72 and 1.76 less kits than previous lines for NBA.

Table 2. Contrasts (SE) of litter size components for comparing different genetic groups with V line.

Contrast	OR	IE	TB	NBA	ES	FS	PS
AA-VV	-0,99(0.58)	-0.53(0.87)	-1.15(0.82)	-1.94(0.81)*	0.04(0.04)	-0,04(0.05)	-0.01(0.05)
AL-VV	-1.30(0.61)*	-0.31(0.92)	-0.74(0.78)	0.08(0.77)	0.07(0.05)	-0.04(0.04)	0.02(0.05)
AH-VV	1.18(0.57)*	1.28(0.85)	1.28(0.72)	1.43(0.71)*	0.03(0.04)	0.02(0.04)	0.04(0.04)
AV-VV	-0.06(0.50)	0.43(0.76)	-0.66(0.65)	-0.25(0.64)	0.04(0.04)	-0.07(0.04)	-0.04(0.04)
LA-VV	0.71(0.61)	1.08(0.92)	-0.42(0.78)	-0.31(0.77)	0.05(0.05)	-0.06(0.04)	-0.04(0.05)
LL-VV	-0.19(0.51)	0.16(0.76)	0.53(0.64)	0.78(0.63)	0.03(0.04)	0.05(0.04)	0.05(0.04)
LH-VV	1.29(0.50)*	0.56(0.74)	0.33(0.75)	-0.28(0.74)	-0.03(0.04)	0.00(0.04)	-0.03(0.04)
LV-VV	-0.48(0.49)	0.09(0.74)	-1.71(0.46)*	-1.34(0.46)*	0.03(0.04)	-0.09(0.03)*	-
HA-VV	0.40(0.58)	0.90(0.87)	0.56(0.74)	0.79(0.73)	0.05(0.04)	0.00(0.04)	0.03(0.04)
HL-VV	-0.04(0.46)	-0.01(0.69)	-0.51(0.59)	0.03(0.58)	0.00(0.03)	-0.02(0.03)	-0.04(0.03)
HH-VV	0.30(0.51)	-0.18(0.76)	0.17(0.63)	-0.27(0.62)	-0.02(0.04)	0.02(0.03)	0.01(0.04)
HV-VV	1.52(0.53)*	1.19(0.79)	0.93(0.67)	1.41(0.66)*	0.00(0.04)	0.00(0.04)	0.00(0.04)
VA-VV	0.57(0.52)	0.98(0.78)	1.05(0.68)	1.54(0.67)*	0.05(0.04)	0.02(0.04)	0.05(0.04)
VL-VV	-0.38(0.52)	-0.86(0.79)	-1.01(0.69)	-0.03(0.69)	-0.04(0.04)	-0.01(0.04)	-0.05(0.04)
VH-VV	0.54(0.52)	0.41(0.78)	0.13(0.69)	0.32(0.68)	0.00(0.04)	0.00(0.04)	0.00(0.04)

[1] OR=ovulation rate; IE=implanted embryos; TB=total born; NBA=number of born alive; ES = embryonic survival; FS = fetal survival; PS= prenatal survival; * significant difference ($P<0.05$).

Favourable and important differences were found between some crossbreds (AH, LH, HA, HV and VH) and purebred V animals for all traits. But crossbred LV showed an important reduction in prolificacy with respect to the V line, which presented low values for TB, NBA, FS and PS. An indication of the importance of using a particular line either as sire or dam was assessed by checking the differences between a particular cross and their reciprocal. Differences between reciprocal crosses reflect differences in gene frequencies between lines for the additive maternal and dominance maternal effects (Eisen *et al.,* 1983). Some relevant differences between reciprocal crosses were observed for OR and TB between lines A and LP, lines A and H, lines A and V, lines LP and H and lines LP and V

indicating that the best performance could be achieved under a particular reciprocal cross, i.e. maternal effects verified.

In general, there are no significant differences in direct genetic effects although the magnitudes of the differences are high for some traits (Table 3). The only significant differences were observed between A and V lines for NBA, favouring V line, and between LP and A lines in favour of the LP line. Differences between LP, H and V lines did not show significant difference. Regarding the maternal genetic effects were only significant for OR, being negative for the LP line with respect to any other line. For direct genetic effects on TB and NBA, Baselga *et al.* (2003) and Orengo *et al.* (2003) found significant differences favouring V line, and the last authors also found significant differences between H and A line, favouring H line. But none of them found any significant maternal genetic effect between these lines.

Table 3. Contrast among lines in terms of direct (D), maternal (M) effects and heterosis (H) for litter size components

Item	OR	IE	TB	NBA	ES	FS	PS
Direct additive:							
A-V	-1.29(0.73)	-0.60(1.01)	-1.88(0.99)	-2.62(0.98)*	0.05(0.05)	-0.09(0.05)	-0.04(0.06)
L-V	0.73(0.66)	1.15(1.06)	0.25(0.83)	-0.22(0.82)	0.04(0.05)	-0.02(0.04)	0.01(0.05)
H-V	0.09(0.64)	0.11(0.97)	-0.43(0.82)	-0.57(0.81)	0.01(0.05)	-0.03(0.04)	-0.02(0.04)
A-L	-2.01(0.78)*	-1.75(1.18)	-2.13(1.06)*	-2.41(1.05)*	0.01(0.06)	-0.07(0.06)	-0.05(0.06)
A-H	-1.38(0.86)	-0.71(1.03)	-1.45(1.16)	-2.05(1.15)	0.04(0.06)	-0.06(0.06)	-0.02(0.07)
L-H	0.64(0.80)	1.03(0.80)	0.68(1.03)	0.36(1.02)	0.03(0.06)	0.02(0.05)	0.03(0.06)
Maternal additive:							
A-V	0.34(0.45)	-0.08(0.67)	0.76(0.58)	0.71(0.57)	-0.01(0.03)	0.06(0.03)	0.03(0.03)
L-V	-0.91(0.44)*	-0.99(0.66)	0.29(0.54)	1.00(0.53)	-0.02(0.03)	0.07(0.03)	0.03(0.03)
H-V	0.10(0.42)	-0.34(0.64)	0.51(0.55)	0.21(0.54)	-0.03(0.03)	0.05(0.03)	0.03(0.03)
A-L	1.25(0.46)*	1.07(0.70)	0.47(0.60)	-0.28(0.59)	0.01(0.03)	-0.01(0.03)	-0.00(0.03)
A-H	0.24(0.46)	0.32(0.49)	0.25(0.60)	0.50(0.59)	0.02(0.03)	0.00(0.03)	0.01(0.03)
L-H	-1.01(0.41)*	-0.65(0.62)	-0.22(0.56)	0.78(0.56)	0.01(0.03)	0.01(0.03)	0.01(0.03)
Direct heterosis:							
AL	0.27(0.49)	0.58(0.55)	-0.28(0.66)	0.45(0.65)	0.03(0.04)	-0.06(0.03)	-0.03(0.04)
AH	1.16(0.50)*	1.47(0.76)*	1.45(0.67)*	2.26(0.66)*	0.03(0.04)	0.02(0.03)	0.03(0.04)
AV	0.71(0.41)	0.96(0.63)	0.71(0.57)	1.56(0.57)*	0.03(0.03)	-0.01(0.03)	0.01(0.03)
LH	0.58(0.43)	0.32(0.65)	-0.51(0.58)	-0.42(0.57)	-0.01(0.03)	-0.05(0.03)	-0.06(0.03)
LV	-0.37(0.38)	-0.47(0.58)	-1.72(0.43)*	-1.15(0.43)*	-0.01(0.03)	-0.08(0.02)*	-0.07(0.02)*
HV	0.88(0.49)	0.90(0.74)	0.47(0.63)	1.03(0.62)	0.02(0.03)	-0.01(0.03)	-0.01(0.03)

[1] OR=ovulation rate; IE=implanted embryos; TB=total born; NBA=number of born alive; ES = embryonic survival; FS = fetal survival; PS= prenatal survival; * significant difference (P<0.05).

Concerning individual heterosis, favourable and significant values were observed between A and H lines. Heterosis is a function of the dominance and the genetic distance (gene frequencies) between the lines involved in the cross. No significant but relevant estimate of direct heterosis between H and V lines was observed although line H was, partly, originated from the V line. The same happened for LP line, with the influence of the V line in its foundation. Individual heterosis for the cross involving LP line was negative for all traits and significant for some of the traits. It is difficult to find a common explanation for these, apparently, contradictory results. There are very few estimates of crossbreeding parameters, referred to embryonic, fetal or prenatal survivals that are significant. Hulot and Matheron (1979) and Brun *et al.* (1992) detected positive and significant heterosis for ovulation rate and prenatal survival with small values.

CONCLUSIONS

Some differences between performances in components of litter size have been observed in simple crosses of different maternal lines. These differences can be related to differences between lines in direct and maternal effects and to heterosis in the crosses. All these effects seem more important for some traits as ovulation rate than for the embryonic, fetal or prenatal survival.

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