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Litter size components in a full diallel cross of four maternal lines of rabbits[1]

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ABSTRACT: A crossbreeding experiment between 4 Spanish maternal lines of rabbits was performed to estimate crossbreeding effects on litter size components. The experiment was designed as a complete diallel cross involving 4 lines selected for litter size at weaning (A, V, H, and LP (L)) and their 12 simple crosses. Does from these 16 genetic groups were distributed among 4 Spanish farms, but only V line was present in all farms, allowing connectivity of the data. A total of 2,015 does in the third, fourth, or fifth gestations were subjected to laparoscopy. The recorded traits were ovulation rate (OR), number of implanted embryos (IE), total born (TB), embryo survival (ES), foetal survival (FS), and prenatal survival (PS). The differences in direct genetic effects, maternal genetic effects, and individual heterosis between the lines were estimated according to Dickerson's model. Line A was significantly inferior to lines V and H, whereas line LP was similar to A line, but for FS and PS, line A showed the best values, followed by line LP. Comparing crossbred groups to line V, significant differences were shown favoring crossbred groups for OR and IE. The crossbred groups presented high implantation rate, but the foetal survival was lower than in V line. Important values for commercial production were presented by some crosses for OR (HV, 1.26 ova), IE (AH, 1.50 embryos; HV, 1.41 embryos), and TB (AH, 0.82 rabbits; HV, 0.78 rabbits). Relevant and significant reciprocal effects were found, especially for OR in all cases except the LV and VL crosses. These differences become nonsignificant in most of the other traits. Regarding direct genetic effects, line A presented lower estimates than the other lines with important values for OR, but the opposite was observed for FS. The maternal effects were significant only for some contrasts in OR and revealed that the LP line was inferior to the others (1.08 ova compared to the A line, 1.23 compared to the H line, and 0.38 compared to the V line). In general, high positive values for heterosis were found in crossbred does for OR and IE. The crosses, where lines A and H were involved, showed significant heterosis. The highest values were obtained by crossing lines A and H (1.18 ova for OR, 1.87 embryos for IE) followed by the cross between lines H and V. Crosses between line LP and the other lines had a negative heterosis for FS and PS.

Key words: crossbreeding components, litter size, maternal lines, ovulation rate, prenatal survival, rabbits

INTRODUCTION

Litter size is an important trait in maternal rabbit lines (García-Ximenez et al., 1996; Gómez et al., 1996). Studying components of litter size may help to better understand its genetic control. Litter size is limited by number of ova produced and depends on fertilization rate and embryonic and foetal mortality. Prenatal mortality is around 30% in rabbits (García and Baselga, 2002; Mocé et al., 2010) and may be reduced by crossbreeding, which is widely accepted in commercial rabbit production. Expected benefits include reduced sensitivity to environmental challenges in crossbreds than parental groups (Mather, 1953), especially due to the heterosis in reproduction traits; exploiting complementarity between parent-stocks; and dissipation of inbreeding accumulated in the parental stocks as they were developed.

Effects of crossbreeding parameters on components of litter size have been estimated in few studies and the results differ depending on the parent-stocks. In mice, Bradford and Nott (1969) reported that heterosis commonly reduced embryonic mortality, although heterosis effects on ovulation rate and foetal mortality were not always detected. In pigs, Bidanel et al. (1990) and Galvin et al. (1993) found important heterosis for prenatal survival but not for ovulation rate in sows, although King and Young (1957) had suggested important dominance effects for ovulation rate. Hulot and Matheron (1979) and Brun et al. (1992) found favorable and significant heterosis—both ovulation rate and prenatal survival—in rabbits.

Ragab and Baselga (2011) previously compared reproductive traits of the 4 maternal lines (A, V, H, and LP) studied here and concluded that these lines appeared to be viable parent-stocks to produce commercial crossbred does. The objective of this study was to compare these lines and their simple crosses, as well to estimate their direct, maternal, and heterosis effects on components of litter size.

MATERIAL AND METHODS

The research protocol was approved by the animal care and use committee of the Polytechnic University of Valencia.

Animals and Management

The experiment was a full diallel cross between 4 maternal lines (A, V, H, and LP) selected for litter size at weaning (Ragab and Baselga, 2011). Their current generations of selection at the start of the experiment were the 41st, 37th, 20th, and 7th, respectively.

The experimental work was performed in 4 Spanish farms with a total of 2,260 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 the Universidad Politécnica de Valencia (farm 4, 360 does). The genetic groups involved in the experiment were the 4 lines (AA, VV, HH, and LL) and their 12 simple crosses (AV, VA, AH, HA, AL, LA, VH, HV, VL, LV, HL, and LH). Note that the first letter refers to the sire line and the second to the dam line, and L is used to identify the LP line. All the crossbreds and V line were raised in farms 1 and 2 (a set of crossbreds in farm 1 and their reciprocal crosses in farm 2); females of groups VV and HH were raised in farm 3; and VV, AA, and LL animals were raised in farm 4. VV group was used as the reference line because it was present in all the farms, allowing connection of the data among farms, but precluding the estimation of the interaction between farm and genetic type.

Table 1. Descriptive statistics of the experimental data

Traits[1]	N	Mean	Minimum	Maximum	SD
OR	2015	15.31	6.00	30.00	2.78
IE	2015	13.28	1.00	27.00	3.12
TB	1854	11.03	1.00	22.00	3.35
ES	2014	0.87	0.06	1.00	0.15
FS	1854	0.83	0.11	1.00	0.19
PS	1854	0.73	0.05	1.00	0.20

[1]OR = ovulation rate; IE = implanted embryos; TB = total born; ES = embryo survival; FS = fetal survival; PS = prenatal survival.

Management of the animals differed slightly across farms. In all farms, the first mating was at around 18 wk of age for males and females. Natural mating was used in farm 3 and 4, while artificial insemination was conducted in farms 1 and 2. Does were served 10–12 d postkindling, and a pregnancy test was performed by abdominal palpation on Day 12 after mating. Therefore, the reproductive rhythm for the does regularly positive to the pregnancy test was 40–42 d in all farms. In farms 1 and 2, does were inseminated with fresh semen coming from the paternal line R (Estany et al., 1992; 10–20 × 10^6 spermatozoa per dose) after an injection of gonadotropin to induce the ovulation (20 U.I.**[AU: Please define U.I. as it is not a standard JAS abbreviation.]**). In farms 3 and 4, the does of each line were mated to bucks of the same line. In all the farms, rabbit females were fed ad libitum on a standard commercial pellet diet.

Traits and Statistical Analyses

The traits studied were ovulation rate (**OR**; defined as the number of corpus luteum in both ovaries), number of implanted embryos (**IE**; measured as the number of implantation sites), total born (**TB**; measured as the total born per litter), embryo survival (**ES**; calculated as IE/OR), foetal survival (**FS**; calculated as TB/IE), and prenatal survival (**PS**; calculated as TB/OR). Records were obtained from does in their third, fourth, or fifth gestation. Females were subjected to a laparoscopy only once in their life, thus only 1 record per animal was available. Laparoscopy was done 11–12 d after mating, following the surgical technique described by Santacreu et al. (1990). A total of 2,015 laparoscopies were performed, distributed as equally as possible between the genetic types present in each farm. Therefore, an average of 106 laparoscopies were performed per genetic type at each farm. The components were recorded by 2 observers.

All traits were analyzed using the following mixed model, assuming that they are mainly determined by the genotype of the does (Piles et al., 2005, 2006; Tusell et al., 2010):

$$Y_{ijkl} = GFYS_i + PO_j + L_k + a_1 + e_{ijkl},$$

Table 2. Contrasts (standard errors) between line groups for litter size components

	OR[1]	IE[1]	TB[1]	ES[1]	FS[1]	PS[1]
AA-HH	-1.54(0.51)*	-0.79(0.62)	0.55(0.58)	0.03(0.04)	0.10(0.04)*	0.12(0.04)*
AA-LL	-0.35(0.42)	0.07(0.51)	0.49(0.47)	0.03(0.03)	0.04(0.03)	0.06(0.03)*
AA-VV	-1.08(0.39)*	-0.76(0.48)	0.68(0.45)	0.01(0.03)	0.12(0.03)*	0.12(0.03)*
HH-VV	0.46(0.33)	0.03(0.40)	0.13(0.36)	-0.02(0.02)	0.01(0.02)	0.00(0.02)
LL-HH	-1.19(0.50)*	-0.86(0.61)	0.06(0.56)	0.00(0.04)	0.06(0.04)	0.06(0.03)*
LL-VV	-0.73(0.37)	-0.82(0.45)	0.19(0.42)	-0.02(0.03)	0.07(0.03)*	0.06(0.02)*

[1]OR = ovulation rate; IE = implanted embryos; TB = total born; ES = embryo survival; FS = fetal survival; PS = prenatal survival; L: LP line; * significant difference (α = 0.05).

where Y_{ijkl} corresponds to the record of the *l*th doe, obtained at the *i*th genetic group-farm-year-season, *j*th parity order, and *k*th physiological state; $GFYS_i$ is the fixed effect resulting from the combination of the genetic group and farm-year-season (129 levels: for i = 1, …, 129); PO_j is the fixed effect of parity order (3 levels: for j = 3, 4, and 5); L_k is the fixed effect of the lactational status of the doe at mating (2 levels: lactating and not lactating: for k = 1 and 2); a_1 is the random additive genetic value of the doe to which the observation corresponds (for l = 1, …, 2,024), and e_{ijkl} is the residual. Variance components for the random effects were estimated by REML, running the remlf90 program (Misztal et al., 2002), and used to obtain generalized least square solutions of GFYS effects and of their error (co)variance matrix. This was done using the blupf90 program (Misztal et al., 2002). From these solutions, the contrasts between the different genetic groups and VV animals, as well as their error (co)variance matrix, were obtained. Finally, from these contrasts, the differences between direct genetic effects of the lines, maternal genetic effects of the lines, and the individual heterosis of the crosses were estimated according to the model of Dickerson (1969) using a generalized least square procedure (Baselga et al., 2003).

RESULTS AND DISCUSSION

Means and standard deviations of the considered traits 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 for OR (Santacreu et al., 2005; Ibáñez et al., 2006; Laborda et al., 2011, 2012), whereas the means for the other traits were higher than those obtained in previous experiments.

Heritability estimates were 0.24, 0.10, 0.12, 0.07, 0.06, and 0.13 for OR, IE, TB, ES, FS, and PS, respectively. García and Baselga (2002), Bolet et al. (1994), Blasco et al. (1993), Piles et al. (2006), and Laborda et al. (2011, 2012) reported similar estimates of heritability for OR, EI, TB, ES, and PS. In contrast, Blasco et al. (1993), Ibáñez et al. (2006), and Laborda et al. (2012) reported higher estimates for FS. The heritability of PS was in agreement with the estimates in other prolific species, such as pigs (Johnson et al., 1999; Rosendo et al., 2007) or mice (Clutter et al., 1990).

The differences between the line groups are given in Table 2. These figures for OR show that A line had lower OR than V and H lines with significant differences (more than 1 ova), but the opposite was observed for PS, where A line was superior to the other lines. These results showed the high capacity of A line to maintain its embryos during the pregnancy. The high OR of H and V lines was expected because the foundation of these lines was done focusing on prolificacy. Line V was founded integrating four specialized maternal lines, and line H was founded following a scheme of selection for hyperprolificacy. Recently, Ragab and Baselga (2011) showed that these foundation criteria affected the performance of the lines. The same pattern was observed in the comparison between the LP line and lines H and V, but the differences were reduced to nonsignificance for TB due

Table 3. Contrasts (standard errors) between crossbred groups and V line[1]

	OR[2]	IE[2]	TB[2]	ES[2]	FS[2]	PS[2]
AL-VV	-0.14(0.26)	0.33(0.32)	-0.14(0.30)	0.04(0.02)*	-0.02(0.02)	0.00(0.02)
AH-VV	0.87(0.27)*	1.50(0.34)*	0.82(0.31)*	0.05(0.02)*	-0.02(0.02)	0.02(0.02)
AV-VV	0.40(0.27)	0.66(0.33)*	0.25(0.31)	0.02(0.02)	-0.01(0.02)	0.00(0.02)
LH-VV	0.80(0.26)*	0.88(0.32)*	0.26(0.31)	0.01(0.02)	-0.03(0.02)	-0.02(0.02)
LV-VV	0.10(0.26)	0.23(0.32)	-0.55(0.31)	0.01(0.02)	-0.05(0.02)*	-0.04(0.02)*
HV-VV	1.26(0.27)*	1.41(0.33)*	0.78(0.31)*	0.02(0.02)	-0.02(0.02)	0.00(0.02)
all-VV	0.55(0.20)*	0.83(0.24)*	0.23(0.23)	0.03(0.01)*	-0.02(0.01)*	-0.01(0.01)

[1]One cross and its reciprocal were considered together. 2OR = ovulation rate; IE = implanted embryos; TB = total born; ES = embryo survival; FS = fetal survival; PS = prenatal survival; All = average of all crossbred; L: LP line; *significant difference (α = 0.05).

Table 4. Contrasts (standard errors) between reciprocal crosses for litter size components

	OR[1]	IE[1]	TB[1]	ES[1]	FS[1]	PS[1]
AL-LA	-1.83(0.40)*	-0.74(0.50)	-0.56(0.46)	0.05(0.03)	-0.01(0.03)	0.04(0.03)
AH-HA	1.35(0.40)*	0.10(0.49)	0.46(0.46)	-0.06(0.03)*	0.03(0.03)	-0.03(0.03)
AV-VA	-1.38(0.39)*	-0.85(0.48)	-0.55(0.44)	0.02(0.03)	0.01(0.03)	0.03(0.03)
LH-HL	1.81(0.37)*	1.00(0.46)*	0.71(0.44)	-0.03(0.03)	-0.02(0.03)	-0.04(0.03)
LV-VL	-0.60(0.37)	0.19(0.45)	1.06(0.44)*	0.04(0.03)	0.07(0.03)*	0.09(0.03)*
HV-VH	1.21(0.42)*	0.73(0.52)	0.66(0.49)	-0.02(0.03)	0.01(0.03)	-0.02(0.03)

[1]OR = ovulation rate; IE = implanted embryos; TB = total born; ES = embryo survival; FS = fetal survival; PS = prenatal survival; L: LP line; *significant difference ($\alpha = 0.05$).

to the superiority of LP on FS and PS. Differences in IE and TB between lines were not significant.

The differences between crossbred groups (the average of a crossbred group and its reciprocal) and V line are presented in Table 3. Concerning OR, when H line participates in the cross, the crossbred groups showed significantly higher value than V line, showing the importance of crossing between different lines to take advantage of heterosis and complementarity between them. The estimated differences between all crossbreds and V line were around 3.6% of the mean for OR and around 6.3% of the mean for IE. Relevant values, referring to V line, were also observed in some crosses for OR (HV, 1.26 ova), IE (AH, 1.50 embryos; HV, 1.41 embryos), and for TB (AH, 0.82 rabbits; HV, 0.78 rabbits). All these findings highlight the importance of using crossbred does in place of purebred animals from a commercial point of view.

The importance of using a particular line either as sire or dam in a cross was assessed by checking the differences between each cross and its 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 (Table 4), but due to the large sampling errors of the estimates, few significant differences were found. For the case of OR, it was observed that is better to use line A as dam when crossing with V and LP lines, whereas when this line is crossed with the H line the highest ovulation rate was achieved when line A was used as sire. Using H line as dam in place of sire in the crosses with LP allowed significant increments for

OR and IE. Regarding the crosses involving V and LP lines, it would be preferable to use the V line as dam because a superiority was shown for TB, which was a consequence of significant differences for both FS and PS. These results are also indicators that V line can have positive maternal effects for these traits.

Table 5 shows the differences between direct genetic effects of the lines according to the Dickerson model. To some extent, a similar pattern to that obtained when comparing the performance between lines (Table 2) was observed for the contrasts between direct effects. Line A showed a significantly inferior direct effect for OR than H and V lines, whereas a superior direct effect was observed for FS and PS. We also observed a superiority of the direct genetic effect of the LP line over H line for FS, and of the same line over the V line for TB. For direct genetic effects on TB, Baselga et al. (2003) and Orengo et al. (2003) found significant differences favoring the V line. The latter authors also found significant differences between H and A line, with a favorable effect of the H line for this trait.

Regarding maternal genetic effects (Table 6), significant effects were observed for OR in favor of lines A and H compared to lines LP and V. Maternal genetic effects for TB were negative for the LP line with respect to any other line. V line showed a favorable maternal effect on TB, ES, FS, and PS compared to any other lines; this superiority being significant in some cases, especially in PS. In previous experiments, Baselga et al. (2003) and Orengo et al. (2003) did not obtain any significant maternal genetic effect on TB in the crosses between A, V, and H lines.

Table 5. Contrasts (standard errors) for direct genetic effects (D) between lines

	OR[1]	IE[1]	TB[1]	ES[1]	FS[1]	PS[1]
D:A-L	-1.45(0.50)*	-0.75(0.62)	-0.24(0.57)	0.04(0.04)	0.04(0.04)	0.06(0.04)
D:A-H	-1.39(0.58)*	-1.02(0.72)	0.52(0.67)	0.01(0.05)	0.11(0.05)*	0.11(0.04)*
D:A-V	-1.79(0.48)*	-1.12(0.54)*	0.80(0.55)	0.03(0.04)	0.15(0.04)*	0.15(0.03)*
D:L-H	0.06(0.56)	-0.27(0.69)	0.76(0.64)	-0.03(0.04)	0.08(0.04)*	0.05(0.04)
D:L-V	-0.35(0.46)	-0.37(0.56)	1.04(0.52) *	-0.01(0.03)	0.11(0.03)*	0.09(0.03)*
D:H-V	-0.40(0.44)	-0.10(0.53)	0.28(0.49)	0.02(0.03)	0.04(0.03)	0.05(0.03)

[1]OR = ovulation rate; IE = implanted embryos; TB = total born; ES = embryo survival; FS = fetal survival; PS = prenatal survival; L: LP line; * significant difference ($\alpha = 0.05$).

Table 6. Contrasts (standard errors) for maternal genetic effects (M) between lines

	OR[1]	IE[1]	TB[1]	ES[1]	FS[1]	PS[1]
M:A-L	1.08(0.28)*	0.81(0.34)*	0.73(0.32)*	-0.01(0.02)	0.01(0.02)	0.00(0.02)
M:A-H	-0.15(0.29)	0.23(0.35)	0.03(0.33)	0.02(0.02)	-0.01(0.02)	0.01(0.02)
M:A-V	0.71(0.27)*	0.36(0.34)	-0.12(0.31)	-0.02(0.02)	-0.03(0.02)	-0.04(0.02)*
M:L-H	-1.23(0.27)*	-0.58(0.33)	-0.70(0.31)*	0.03(0.02)	-0.02(0.02)	0.01(0.02)
M:L-V	-0.38(0.27)	-0.45(0.33)	-0.85(0.32)*	-0.01(0.02)	-0.04(0.02)*	-0.04(0.02)*
M:H-V	0.85(0.28)*	0.13(0.35)	-0.15(0.33)	-0.04(0.02)*	-0.02(0.02)	-0.05(0.02)*

[1]OR = ovulation rate; IE = implanted embryos; TB = total born; ES = embryo survival; FS = fetal survival; PS = prenatal survival; L: LP line; * significant difference (α = 0.05).

The results indicate that the range of variation of the estimated heterosis between pairs of lines is relatively wide and includes negative values in some traits, particularly in FS and PS for all combinations of the lines (Table 7). Consequently, for TB, some heterosis estimates were negative even though the estimates for OR, IE, and ES were always positive. None of the estimated heterosis effects for TB were significantly different from zero, and the only relevant negative values were observed for the cross between LP and V lines. Favorable individual heterosis effects with significant values were observed for all the crosses for OR and IE, except the crosses between lines LP and V. Regarding FS and PS, only the crosses between lines H and V did not show significant heterosis, but for these traits the heterosis estimated was negative, unfavorable. It seems that in general the cross has affected OR positively and FS and PS negatively, i.e., losses from implantation to parturition are higher in crossbred than in purebred animals, and the magnitude of these differences is higher than the differences between crossbreed and purebred for IE. It is important to note that no heterotic effect was detected for ES in any cross.

Expressed as percentage of the means of the lines involved in the cross, the estimated heterosis ranged between 7.7 and 2.2% for OR, 14.1 and 4.6% for IE, 6.4 and −5.6% for TB, 5.7 and 2.3% for ES, -3.5 and -13.1 for FS, and 0.0 and -10.8 for PS.

There are very few estimates of crossbreeding parameters for litter size components in the literature. In rabbits, Hulot and Matheron (1979) and Brun et al. (1992) detected positive and significant heterosis for ovulation rate and prenatal survival. Baselga et al. (2003) found

significant heterosis in AH and AV for TB but with smaller values than the ones obtained in our study, whereas the very low heterosis values found in HV were not significant. In another study involving a cross between the INRA 2066 and the V lines to form the INRA 2666 line, Brun and Baselga (2005) found significant heterosis for TB and number born alive with similar values to the one obtained in the crosses between A and H lines in our study. In mice, Falconer and Roberts (1960) and Boshier (1968) performed studies to determine 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 foetal survival. However, only the inbreeding experiment reported by McCarthy (1967) showed evidence of dominance in genes affecting foetal survival. Under the theory of dominance, heterosis is a function of the genetic distance (gene frequency differences) between the lines involved in the cross and the dominance parameter (Falconer and Mackay, 1996). In swine, King and Young (1957) suggested a considerable degree of dominance for genes affecting ovulation rate, whereas Galvin et al. (1993) did not observe individual heterosis for ovulation rate and embryo survival, although they concluded that crossbred sows had a very high level of foetal survival compared with purebred females.

Conclusions

Important differences in litter size components have been observed in simple crosses of different maternal lines, some of which could be related to the different

Table 7. Estimates (standard errors) of the heterosis (H) between pair of lines

	OR[1]	IE[1]	TB[1]	ES[1]	FS[1]	PS[1]
H:AL	0.78(0.37)*	1.15(0.45)*	-0.55(0.47)	0.04(0.03)	-0.11(0.03)*	-0.08(0.03)*
H:AH	1.18(0.38)*	1.87(0.46)*	0.44(0.43)	0.05(0.03)	-0.08(0.03)*	-0.04(0.03)
H:AV	0.87(0.33)*	1.04(0.41) *	-0.08(0.38)	0.02(0.02)	-0.07(0.02)*	-0.06(0.02)*
H:LH	0.88(0.36)*	1.29(0.44*	0.09(0.41)	0.03(0.03)	-0.07(0.03)*	-0.05(0.02)*
H:LV	0.34(0.32)	0.61(0.39)	-0.65(0.37)	0.03(0.02)	-0.08(0.02) *	-0.06(0.02)*
H:HV	0.98(0.31)*	1.36(0.39)*	0.71(0.36)	0.03(0.02)	-0.03(0.02)	0.00(0.02)

[1]OR = ovulation rate; IE = implanted embryos; TB = total born; ES = embryo survival; FS = fetal survival; PS = prenatal survival; L: LP line; * significant difference (α = 0.05).

ways in which lines were founded. Particularly, the crosses involving line H, founded on hyperprolificacy, exhibited the highest values in ovulation rate, implanted embryos, and total born alive. Ovulation rate was the trait most influenced by the reciprocal effects. There were some significant differences in direct genetic effects. The maternal genetic effects were mainly important for ovulation rate, in agreement with the results for the reciprocal effects. The heterosis estimates were always favorable and positive for ovulation rate and implanted embryos, while unfavorable and negative for foetal and prenatal survival. Embryo survival did not show any significant heterotic effect.

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