

GENETIC ANALYSIS OF GROWTH TRAITS IN THE PROGENY OF RABBIT DOES FROM A DIALLEL CROSS

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Abstract: An experiment was carried out to estimate the genetic group effects and the crossbreeding genetic parameters of growth traits [body weight (BW), average daily gain (ADG), feed intake (FI) and feed conversion ratio (FCR)] in rabbits during fattening between 28 and 63 d. The rabbits were the progeny of does coming from a full diallel cross between 4 maternal lines (A, V, H and LP) mated to bucks of the paternal line R. On thousand fifty five rabbits were controlled and the traits were recorded weekly, with the cage as the experimental unit for FI and FCR (283 cages). The genetic group (V line) was present in all farms in order to connect records among them and to be used as reference group. Crossbreeding parameters were estimated according to the Dickerson model. Regarding dam effects between pure lines for BW at weaning, A line was the heaviest and showed significant differences with LP and V lines (61 and 30 g, respectively). Upon completion of the fattening period, the differences in favour of A line for BW at weaning were compensated. Throughout the fattening period, no significant differences were observed between the lines as dam lines. At the end of the fattening period, no significant differences were observed between the crossbred groups. Regarding the reciprocal effects, the most relevant results were the significances for FCR in favour of H as sire line. For all traits, the confidence intervals at 95% of all contrast and effects were large. The estimates of maternal heterosis were, in general, negative, which could be a consequence of the positive heterosis for litter size. The AH cross showed significant maternal heterosis for BW at 43 d (-53 g), ADG between 28 and 42 d (-3.5 g/d), FI between 28 and 63 d (-7 g/d) and FCR between 42 and 63 d (-0.15). The combination of direct and maternal effects of the V line was the worst for all growth traits, showing significant differences with the LP line for most of them, for instance 0.13 worse FCR between 28 and 63 d. Grand-maternal effects were less important than direct-maternal.

Key Words: crossbreeding parameters, diallel cross, growth traits, maternal lines, rabbits.

INTRODUCTION

Postweaning average daily gain (ADG), feed intake (FI) and feed conversion ratio (FCR) are important traits in meat rabbit production, since postweaning feeding accounts for around 30-40% of the total production cost (Baselga and Blasco, 1989; Cartuche *et al.*, 2013). Individual FCR is expensive to measure, both in facility needs and in labour. On the contrary the growth rate, estimated as the daily gain between weaning and slaughter, is much cheaper, easier to measure and is moderately and negatively correlated with FCR (Piles *et al.*, 2004a). Postweaning ADG has traditionally

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been used as selection criterion to indirectly improve FCR. These selection procedures exploit genetic variability within populations, in this case paternal lines. But important differences between populations have also been shown to exist for these traits (Larzul and Rochambeau, 2004). Breeders exploit variability by crossing animals from different lines.

Rabbit meat is principally produced following a 3-way crossbreeding scheme, using crossbred females which are mated to sires from a paternal line selected for growth traits (Rochambeau, 1988; Baselga, 2004). These females are expected to show better reproductive performance than the average of the does of the parental lines due to the advantage of heterosis and complementarity in reproductive traits (Khalil *et al.*, 1995; Orengo *et al.*, 2003; Ragab, 2012).

Traditionally instead, only reproductive or maternal traits are considered during the selection of the lines to be used in obtaining crossbred females, however these females contribute with half of the genome of slaughter animals, thus growth characteristics of these lines are also relevant.

The objective of this work was to estimate genetic group differences and crossbreeding parameters for growth traits of rabbits, the dams of which come from a full diallel-cross among four maternal lines and the sires from a paternal line.

MATERIAL AND METHODS

Animals

The present study involved animals, the dams of which came from a full diallel cross among four maternal lines (A, V, H and LP) and the sires from a single paternal line (R). The maternal genetic groups involved in the experiment were 4 pure lines (AA, VV, HH and LL) and 12 single crosses (AV, VA, AH, HA, AL, LA, VH, HV, VL, LV, HL and LH). The first letter of the genetic group name corresponds to the sire line and the second one to the dam line name. L is used to identify the LP line as sire or dam of a genetic group.

The animals of A, V and LP lines were maintained as closed nucleus populations from the beginning of the selection process for prolificacy until the present and were housed on the farm of the Animal Science Department, Universitat Politècnica de València (UPV), and the current generation of these lines are 43rd, 38th and 8th, respectively. The H line was housed on the same farm until its 10th generation of selection (May, 2004) when it was moved to another farm 180 km north of Valencia (San Càrles de la Rápita, Tarragona), this line is now in its 22nd generation of selection.

Line A was originated in 1980 from New Zealand White (NZW) rabbits reared by farmers near Valencia, Spain. The NZW breed has been commonly accepted as one of the main rabbit breeds used for meat production. The criteria used to form line A were that the founders were healthy and fulfilled the standards of the NZW breed. Since 1980, the line has been selected for prolificacy at weaning by using a family index (Estany *et al.*, 1989). Line V was established from 4 different synthetic populations in 1984. Selection candidates are also genetically evaluated for prolificacy at weaning using a repeatability animal model, obtaining BLUP predictions of their additive genetic value (Estany *et al.*, 1989), the same procedure of selection is used for H and LP lines. Line H was founded by applying hyperprolific selection and embryo cryopreservation techniques (Cifre *et al.*, 1998). The hyperprolific does, used in founding this line, were assembled from several large commercial populations. The LP line was founded by selecting females from commercial farms that showed an extremely long productive life associated with prolificacy near or above the average of the Spanish commercial rabbit population (Sánchez *et al.*, 2008).

For all the lines, does for the next generation are selected from 25-30% of the best evaluated matings, with a limit of 4 does by mating. The bucks are selected within sire from the best mating of the sire to contribute a son to the next generation. Selection is in non-overlapping generations for all lines.

Line R was derived from the synthetic cross of 2 paternal lines in 1988, one founded in 1976 with California rabbits and the other one founded in 1981 with rabbits from a terminal sire line (Estany *et al.*, 1992). The selection process for postweaning daily gain from 28 to 63 d is in its 32nd generation; in this case selection candidates are genetically evaluated exclusively based on their phenotype, i.e. individual selection. Each sire contributes a male offspring to the next generation and does are selected weekly at a rate of around 20%, taking into account the average growth of the

previous 4 wk. Selection was in non-overlapping generations until the 25th generation. The selection of this line is in overlapping generations from generation 25th to the present.

In all the lines, does are mated for first time around 17 wk of age and then serviced 10–12 d post-kindling and a pregnancy test is carried out by abdominal palpation on day 12 after mating. Does which did not accept the buck were presented to the male 1 wk later and does that were not diagnosed as pregnant after abdominal palpation, were also returned to the male for a repeat mating. Currently, animals of these lines are used as maternal grandparents (lines A, V, H and LP) or as terminal bucks (line R) in 3-way crosses in commercial Spanish rabbit meat production. The UPV and the Institut de Recerca i Tecnologia Agroalimentaries (IRTA) have established a network of selection-multiplication centres from which the lines are made available to commercial farms (Baselga, 2004).

Crossbreeding Design and Management

The study was carried out on 4 different farms, located in Altura (Castellón, Spain), Rioseco de Tapia (León, Spain), Valencia (Spain) and Sant Carles de la Ràpita (Tarragona, Spain). In each farm, the same experimental design was performed. The distribution of the does in the farms is shown in Table 1; the genetic group VV was present on all farms allowing data connection between farms. However, because this was the only genetic type across all the farms, no interaction between farm and genetic type could be considered.

Twenty five females from each genetic group on the different farms were inseminated by bucks of the R line to ensure a sufficient number of young rabbits at weaning (at 28 d of age). At weaning, 120 young rabbits of each genetic group were randomly sampled, avoiding whole litters. The young rabbits were individually identified by a number tattooed on the ear and placed in collective cages of eight individuals until marketing at 63 d of age. Steps were taken to ensure that all animals in the same cage did not belong to the same litter, but they always belonged to the same genetic group. During the post-weaning period, rabbits were fed *ad libitum*, with a standard commercial pellet diet and fresh water.

The whole fattening period lasted 5 wk on all the farms. On the farm in Altura, it took place from February 1st 2011 to March 8th 2011; at Rioseco de Tapia from May 9th 2011 to June 13th 2011; in UPV from February 21st 2012 to March 27th 2012, and at San Carles de la Ràpita from April 24th 2012 to May 29th 2012.

No serious health problems were observed throughout the experiment, but the mortality rate (14%) was higher than expected on a commercial farm, this rate was unequal across genetic groups, thus the distribution of animals by genetic group was unbalanced. The noted high mortality could be a consequence of the intense weekly manipulations of such young rabbits for the collection data.

Data Recording and Statistical Model

Individual rabbit weights and cage feed consumption were recorded weekly. The cage was the experimental unit for feed intake (FI g/d) and feed conversion ratio (FCR). FI was recorded at the cage level, keeping the same management conditions as in the commercial farms. Other alternatives for assessing FI would be to keep animals in individual cages, but this situation is far from the management practices conducted in commercial facilities. However, Feki *et al.* (1996) and Orengo *et al.* (2009) studied growth traits in rabbit. They compared individual cage and collective cage of 8 animals. No major differences were noticed for these traits for both types of housing. This similarity may support the cage approach for estimating individual FI and FCR.

Table 1: Localisations of the genetic groups of the does.

Grand-sire line	Grand-dam line			
	A	H	LP	V
A	UPV ¹	Altura	Rioseco ²	Rioseco
H	Rioseco	San Carles ³	Rioseco	Altura
LP	Altura	Altura	UPV	Rioseco
V	Altura	Rioseco	Altura	ALL ⁴

¹Universitat Politècnica de València. ²Rioseco de Tapia. ³San Carles de la Ràpita. ⁴In all the farms.

Body weight (BW, g) was considered at 28 (BW₂₈), 42 (BW₄₂) and 63 (BW₆₃) days of age. These days correspond to the day of weaning, the end of the 2nd wk of fattening, and the slaughter day, respectively. Individual average daily gain (ADG, g/d), FI and FCR were defined in addition to the overall fattening period (ADG₂₈₋₆₃, FI₂₈₋₆₃, FCR₂₈₋₆₃), for the first 2 wk of growth (ADG₂₈₋₄₂, FI₂₈₋₄₂, FCR₂₈₋₄₂) as well as for the last 3 wk of fattening (ADG₄₂₋₆₃, FI₄₂₋₆₃, FCR₄₂₋₆₃).

In order to properly account for the number of live animals in a cage when computing FI it was also necessary to record the date of any young rabbit deaths. In this analysis only data from rabbits alive at the end of the week were considered, thus feed consumed by the dead rabbits during the week when they died was predicted and then subtracted from the total feed intake recorded for that week and cage. FI was obtained by dividing the corrected total cage feed intake by seven times the number of rabbits alive at the end of the week. Finally, in order to compute the FI variables which were to be analysed (FI₂₈₋₄₂, FI₄₂₋₆₃ and FI₂₈₋₆₃) the FI for the corresponding weeks were added and divided by the number of weeks in the relevant period. FI from cages in which more than 2 rabbits died in a week were discarded for that particular week. The prediction for the amount of feed ingested by a rabbit at a given day (x) of fattening was based on a quadratic predictive equation adjusted to each farm. These predictive equations were obtained after a least squares adjustment of the average daily feed consumption per rabbit in any given week on the farm to the middle day of that week (3.5, 10.5, 17.5, 24.5 and 31.5 d). This average daily feed consumption was computed by dividing the total amount of feed ingested on the farm during the week by the total number of rabbit-days eating that week. Each live rabbit at the week's end contributes 7 d to the total number of rabbit-days, but it is assumed that dead rabbits do not consume for a few days prior to death, so the number of days is arrived at according to the difference between death weight and the previous recorded weight. When a rabbit did not lose weight or the loss was lower than 100 g, it was assumed that it had been consuming normally until the day of death. On the contrary, when the loss is between 100-200 g, 200-300 g or higher than 300 g it was assumed that during 2, 3 and 4 d, respectively, before death the rabbit had not eaten. Consequently, a dead rabbit contributes to the total with the number of days alive during the week minus the number of days of not eating before its death.

The estimated equations were:

$$FI = -0.07x^2 + 6.02x + 53.17, \text{ for Altura} \quad (\text{Equation 1})$$

$$FI = -0.05x^2 + 5.29x + 53.33, \text{ for Rioseco de Tapia} \quad (\text{Equation 2})$$

$$FI = -0.12x^2 + 7.60x + 49.10, \text{ for San Carlos de la Rápita} \quad (\text{Equation 3})$$

$$FI = -0.04x^2 + 5.51x + 57.60, \text{ for UPV} \quad (\text{Equation 4})$$

Where x is the day of the fattening period, 1 to 35. By using these equations it was assumed that the normal feed consumption of one rabbit depends exclusively on the age of the animal and the farm where fattening is taking place. The calculation of the amount of feed consumed by a dead rabbit before its death was obtained by applying the former equations to the days of fattening while the rabbit was alive. Finally, the corrected total cage feed intake was obtained by subtracting the sum of all daily FI predictions for dead rabbits, previous to their death, from the total cage feed intake.

Once FI and ADG have been calculated for each cage and period, the corresponding value for FCR is obtained dividing the FI of the period by ADG of it.

The model used in the analysis of ADG and BW was:

$$Y_{jkd} = GG_j + F_k + S_i + e_{jkd} \quad (\text{Equation 5})$$

Where: Y_{jkd} is a record of the trait; GG_j is the effect of genetic group (16 levels); F_k is the effect of the farm (4 levels); S_i is the effect of the sex and e_{jkd} is the residual effect.

The model (Equation 5) for the analysis of FCR and FI was the same without the sex effect; in this case the experimental unit was the cage.

Estimates of the differences between all the genetic groups and VW animals were obtained by generalised least squares, using the program blupf90 (Misztal *et al.*, 2002), along with the estimates of the error (co)variance matrix between these estimates. The residual variances required to solve the models were estimated in a previous REML step. Crossbreeding genetic parameters (direct, maternal and grand-maternal additive genetic effects, individual and

maternal heterosis) were considered according to the model proposed by Dickerson (1969), to explain the expected means of the genetic groups.

In the study, the dams of the rabbits came from a full diallel cross among four maternal lines, and their sires come from the same paternal R line. Thus, there were 5 different types of genetic parameters: direct additive genetic effects (G_i^D , i=A, V, H, L, R), maternal additive genetic effects (G_i^M , i=A, V, H, L), grand-maternal genetic effects ($G_{ij}^{M'}$, i=A, V, H and L), individual heterosis (H_{Ri}^I , i=A, V, H, L) and maternal heterosis (H_{ij}^M , i≠j, i=A, V, H, L and j=A, V, H, L). These genetic parameters cannot be estimated individually; however, the following functions of them can be estimated:

a) Direct-maternal differences between lines,

$$G_{i-j}^I = \frac{1}{2}(G_i^D - G_j^D) + (G_i^M - G_j^M) + (H_{Ri}^I - H_{Rj}^I), i \neq j, i=A, V, H, L \text{ and } j=A, V, H, L \quad \text{(Equation 6)}$$

b) Grand-maternal differences between lines,

$$(G_{i-j}^{M'} = G_i^{M'} - G_j^{M'}), i \neq j, i=A, V, H, L \text{ and } j=A, V, H, L \quad \text{(Equation 7)}$$

c) Maternal heterosis, previously defined.

Estimable functions of the crossbreeding parameters were obtained adjusting by generalised least squares the estimates of the genetic groups effects (as contrasts to the V line) to the coefficients described in Table 2. In this generalised least squares procedure the error (co)variance matrix between the estimates of the genetic group effects was used as weighting matrix (Baselga *et al.*, 2003). Wald tests were performed to test for significance.

RESULTS AND DISCUSSION

Descriptive Statistics

Summary statistics for all traits are shown in Table 3. The mean slaughter weight (BW₆₃) is within the range of commercial weights in Spain (between 2000 and 2300 g). Fl₂₈₋₆₃ raw average was 127 g/d, this figure is lower than

Table 2: Coefficients for computing estimable functions of the crossbreeding parameters from the differences of the doe genetic groups to line V.

Estimable Function	¹ A×A	A×L	A×H	A×V	L×A	L×L	L×H	L×V	H×A	H×L	H×H	H×V	V×A	V×L	V×H
² G _{A-V} ^I	1	0.5	0.5	0.5	0.5	0	0	0	0.5	0	0	0	0.5	0	0
G _{L-V} ^I	0	0.5	0	0	0.5	1	0.5	0.5	0	0.5	0	0	0	0.5	0
G _{H-V} ^I	0	0	0.5	0	0	0	0.5	0	0.5	0.5	1	0.5	0	0	0.5
³ G _{A-V} ^{M'}	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0
G _{L-V} ^{M'}	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0
G _{H-V} ^{M'}	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1
⁴ H _{A-L} ^M	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
H _{A-H} ^M	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
H _{A-V} ^M	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
H _{L-H} ^M	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
H _{L-V} ^M	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
H _{H-V} ^M	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1

¹ Genetic group, X×Y; X= sire line of the doe; Y dam line of the doe; L=LP line. ² G_{X-V}^I: direct-maternal differences between line X and line V. ³ G_{X-V}^{M'}: grand-maternal differences between lines X and V (see text for complete explanation). ⁴ H_{X-Y}^M: maternal heterosis between lines X and Y.

Table 3: Descriptive statistics for body weight (¹BW, g), average daily gain (²ADG, g/d), individual feed intake (³FI, g/d) and feed conversion ratio (⁴FCR).

	⁵ n	Mean	⁶ SD	Maximum	Minimum
BW ₂₈	2273	615	118	1070	310
BW ₄₂	2076	1226	200	1830	480
BW ₆₃	1955	2215	275	3110	840
ADG ₂₈₋₄₂	2076	44.1	8.3	71.4	9.3
ADG ₄₂₋₆₃	1955	46.6	6.9	70.9	10.9
ADG ₂₈₋₆₃	1955	45.6	5.8	63.4	11.1
FI ₂₈₋₄₂	283	90	9	120	67
FI ₄₂₋₆₃	283	151	15	197	100
FI ₂₈₋₆₃	283	127	11	160	89
FCR ₂₈₋₄₂	283	2.07	0.24	2.90	1.51
FCR ₄₂₋₆₃	283	3.29	0.27	4.30	2.44
FCR ₂₈₋₆₃	283	2.79	0.21	3.51	2.28

¹ BW_x, body weight at day x of age. ² ADG_{x-y}, average daily gain between days x and y. ³ FI_{x-y}, individual feed intake between days x and y per day. ⁴ FCR_{x-y}, feed conversion ratio between days x and y. ⁵ n=number of rabbits or cages. ⁶ SD= standard deviation.

the mean of FI for the fattening period in Spain, which is 135 g/d, but this average was obtained with slaughter at 66 d (MAGRAMA, 2012).

For ADG and FCR, raw averages were 45.7 g/d and 2.79 respectively. Carabaño (2000) reported a higher FCR value (3.2) in a study where the weaning and slaughter ages were not specified. Weaning weight (BW₂₈) raw averages were lower compared to the results from the same lines reported by Orengo *et al.* (2009) in a study where the rabbits were weaned at 32 d. However, BW₆₃, ADG₂₈₋₆₃, FI₂₈₋₆₃ and FCR₂₈₋₆₃ were higher than in Orengo *et al.* (2009). On the one hand, the slaughter age in our experiment was 63 d, being 60 d in their study; on the other, the sire of the rabbits belonged to a line selected for growth rate, while in their experiment the rabbits themselves, not the dams, came from a complete 5 diallel cross between 3 maternal and 2 paternal lines, therefore not all the parents of the young rabbits came from lines selected for growth traits. Piles *et al.* (2004b) obtained higher values for all growth traits (BW₆₃, ADG₂₈₋₆₃, FI₂₈₋₆₃ and FCR₂₈₋₆₃), in a study considering Caldes line (IRTA), R line (JPV) and their simple crossbreds, where both lines are paternal lines selected for growth traits (litter weight at weaning and individual daily weight gain between 32 and 60 d of age for Caldes line and daily gain between 28 and 63 d for R line, as previously explained).

Differences between genetic groups

The contrasts between the dam effects of the lines for the studied traits can be observed in Table 4. Differences in weaning weight are economically important because there is a negative relationship between weaning weight and mortality during the fattening period (Morisse, 1995; Rashwan and Marai, 2000). For this trait (BW₂₈) differences were observed in favour of line A (significant with L and V). Orengo *et al.* (2004) reported that higher body weights at weaning were obtained when litter size at birth was lower; thus the differences we observed can be explained because fattened rabbits from the A line came from litters with the lowest number born alive (BA, 10.13) and the lowest number of weaned rabbits (NW, 8.76). These findings regarding BA and NW are in agreement with results by Ragab and Baselga (2011), they clearly observed that lines V, L and H showed superiority over line A for both BA and NW.

In our study, the contrasts involving the V line, which was the lightest at weaning (significant with L), cannot be explained by differences in prolificacy (11.56 BA and 9.96 NW, in the V line), as line LP had higher prolificacy (12.30 BA and 10.56 NW) and also showed higher BW₂₈. El Nagar *et al.* (2013) observed that V line was that producing less milk; and body weight at weaning has been shown to be associated with milk production (McNitt and Lukefahr, 1990). During the fattening period (BW₄₂), the differences in favour of line A decreased, but on the contrary, the difference of the V line compared to the other lines was maintained (the contrasts A-V and LP-V remained

Table 4: Contrasts (standard error) between the lines for body weight (¹BW, g), average daily gain (²ADG, g/d), individual feed intake (³FI, g/d) and feed conversion ratio (⁴FCR).

	A-H	A-LP	A-V	H-V	LP-H	LP-V
BW ₂₈	37(20)	30(14)*	61(14)*	23(14)	6(20)	30(14)*
BW ₄₂	17(41)	-26(29)	60(29)*	42(29)	43(40)	85(28)*
BW ₆₃	-20(50)	-17(36)	40(36)	60(36)	-3(49)	57(34)
ADG ₂₈₋₄₂	-0.1(1.6)	-3.5(1.0)*	0.2(1.1)	0.4(1.1)	3.3(1.6)*	3.7(1.1)*
ADG ₄₂₋₆₃	-2.1(1.3)	-0.3(1.0)	-1.3(0.9)	0.7(0.9)	-1.8(1.3)	-1.0(0.9)
ADG ₂₈₋₆₃	-1.2(1.1)	-1.4(0.8)	-0.7(0.7)	0.5(0.7)	0.2(1.0)	0.7(0.7)
FI ₂₈₋₄₂	0(4)	-6(3)*	2(3)	2(3)	6(4)	8(3)*
FI ₄₂₋₆₃	-4(6)	-2(5)	3(5)	7(5)	-2(6)	5(5)
FI ₂₈₋₆₃	-2(5)	-4(3)	2(3)	5(3)	1(5)	6(4)
FCR ₂₈₋₄₂	0.08(0.08)	0.06(0.06)	0.08(0.06)	0.00(0.06)	0.02(0.08)	0.02(0.06)
FCR ₄₂₋₆₃	0.07(0.12)	-0.01(0.08)	0.15(0.08)	0.08(0.08)	0.08(0.11)	0.15(0.08)
FCR ₂₈₋₆₃	0.06(0.07)	0.03(0.05)	0.09(0.05)	0.05(0.05)	0.03(0.07)	0.08(0.05)

¹ BW_x, body weight at day x of age. ² ADG_{x-y}, average daily gain between days x and y. ³ FI_{x-y}, individual feed intake between days x and y per day. ⁴ FCR_{x-y}, feed conversion ratio between days x and y. *P<0.05 (significant difference at α=0.05).

significant in the same direction). At the end of the fattening period, the differences in favour of A line for weight at 28 d were compensated, and BW₆₃ for lines H and LP were the highest. This result is in agreement with those observed by Mínguez *et al.* (2012), who showed that H and LP lines were the heaviest both at weaning and at 63 d of age at foundation and also nowadays after the selection process. The relationship between BW, ADG and FI for the whole fattening period can be observed in Table 4. If the difference of a contrast between BW₂₈ and BW₆₃ was reduced, the sign of the corresponding contrast for ADG₂₈₋₆₃ was negative, being positive when the difference of the contrast between BW₂₈ and BW₆₃ was increased. An increase in ADG was caused by a greater FI, as reported by Ouhayoun (1978). Significant differences in FCR were not observed, but V line tended to have the lowest FCR. This can be observed in the contrast A-V and LP-V, principally during the last part of the fattening FCR₄₂₋₆₃, but also for the whole fattening period FCR₂₈₋₆₃.

For A and V lines, we obtained similar results for BW₂₈, FCR₂₈₋₄₂ and FCR₂₈₋₆₃ to those of Feki *et al.* (1996) who showed superiority of line A over line V for BW₂₈, and no significant differences in FCR₂₈₋₄₂ and FCR₂₈₋₆₃. However, for ADG₂₈₋₄₂, ADG₂₈₋₆₃, FI₂₈₋₄₂ and FI₂₈₋₆₃ they showed a superiority of line V, superiority not confirmed in our study.

Although no significant differences were observed throughout the fattening period for all growth traits, the great length of the confidence intervals at 95% should be taken into account. Perhaps there were relevant differences between lines that could not be detected given our extremely large errors. The maximum differences, according to the confidence interval at 95%, would be -119 g for BW₆₃ (contrast A-H), -3.3 g/d for ADG₂₈₋₆₃ (contrast A-H), 12 g/d for FI₂₈₋₆₃ (contrast LP-V) and 0.20 for FCR₂₈₋₆₃ (contrast A-H). The magnitudes of these figures are expected to have important economic consequences.

In commercial farms, crossbred does are the most common type of females and, consequently, some differences for growth traits in dam effects might have an economic impact. Consequently, let us consider the different crossbred groups (the average of a cross and its reciprocal) with respect to the V line (Table 5). Crossbreds involving A line were significantly heavier at weaning (BW₂₈); once again, these results could partially be explained by invoking differences in prolificacy, crossbred does AH and AL had lower BA (10.80 and 10.69, respectively) than V animals (11.15) on the Altura and Rioseco de Tapia farms. This explanation does not hold for AV crossbred does, which had higher BA than V does. In this case, the significant difference in favour of the AV is perhaps due to the aforementioned lower milk production of the V line.

Table 5: Contrasts (standard error) between crossbred genetic groups¹ and V line for body weight (²BW, g), average daily gain (³ADG, g/d), individual feed intake (⁴FI, g/d) and feed conversion ratio (⁵FCR).

	¹ AH-VV	AL-VV	AV-VV	HV-VV	LH-VV	LV-VV	All-VV
BW ₂₈	26(10)*	44(10)*	31(10)*	6(10)	15(10)	11(10)	22(8)*
BW ₄₂	-12(19)	4(19)	-5(19)	6(19)	3(20)	-10(20)	-2(15)
BW ₆₃	-22(26)	28(26)	2(27)	-2(26)	28(26)	-6(27)	4(20)
ADG ₂₈₋₄₂	-2.1(0.8)*	-2.3(0.8)*	-2.7(0.8)*	-0.7(0.8)	-0.9(0.8)	-1.5(0.8)	-1.7(0.6)*
ADG ₄₂₋₆₃	0.4(0.7)	2.4(0.7)*	1.1(0.7)	0.3(0.7)	1.1(0.7)	0.6(0.7)	1.0(0.5)
ADG ₂₈₋₆₃	-1.0(0.5)	0.3(0.5)	-0.8(0.6)	-0.1(0.6)	0.3(0.6)	-0.4(0.6)	-0.3(0.4)
FI ₂₈₋₄₂	0(2)	1(2)	-1(2)	0(2)	4(2)*	-1(2)	1(2)
FI ₄₂₋₆₃	-3(3)	-2(3)	-1(3)	-1(3)	-0(3)	-6(3)*	-2(2)
FI ₂₈₋₆₃	-2(2)	-1(2)	-1(2)	-1(2)	1(2)	-4(2)	-1(2)
FCR ₂₈₋₄₂	0.14(0.04)*	0.18(0.04)*	0.15(0.04)*	0.01(0.04)	0.12(0.04)*	0.07(0.04)	0.11(0.03)*
FCR ₄₂₋₆₃	-0.13(0.06)*	-0.17(0.06)*	-0.13(0.06)*	-0.02(0.06)	-0.11(0.06)	-0.07(0.06)	-0.10(0.04)*
FCR ₂₈₋₆₃	0.01(0.04)	0.00(0.03)	0.02(0.03)	-0.01(0.04)	0.00(0.03)	0.00(0.03)	0.00(0.03)

¹ One cross and its reciprocal are considered together. ² BW_x, body weight at day x of age. ³ ADG_{x-y}, average daily gain between days x and y. ⁴ FI_{x-y}, individual feed intake between days x and y per day. ⁵ FCR_{x-y}, feed conversion ratio between days x and y. All-VV: the contrast between all crossbred and V line. L: LP line. *P<0.05 (significant difference at $\alpha=0.05$).

It might be expected that the crossbred dams would show a better performance than line V mothered animals. However, as happened in the contrast between lines (Table 4), no significant differences were observed over the whole fattening period for all growth traits. Significant differences in certain weeks are compensated in the whole fattening period. In this sense it can be noted that the crosses that had advantage over the line V for BW₂₈ had a subsequent growth rate worse than the V line. Such is also the situation when crossbreds are considered together (All-VV). It seems that a compensatory growth has taken place after weaning; this process has previously been shown in rabbits by Testik *et al.* (1999) and Belhadi (2004). This compensatory growth is expected because maternal effects lose importance after weaning (Minguez, 2011) and ADG is relatively free of maternal effects (Estany *et al.* 1989; Camacho and Baselga, 1991; Cifre *et al.* 1999; Su *et al.* 1999). It must also be noted that the pattern of the contrast for ADG₄₂₋₆₃ was opposite to that for ADG₂₈₋₄₂, all the estimates for the last one being positive, but only significant for the contrast AL-VV.

Contrarily to the comparisons between lines, in the contrasts between crossbreds it was common to find the association of negative contrast for FI with positive contrast for ADG and the opposite. This outcome could explain the significant contrasts observed for FCR in the first 2 wk and the last 3 wk of fattening, but the most important factor determining the results for FCR seems to be linked to ADG. Thus, practically always, if for a period the effect of a crossbred is superior (inferior) to the effect of the V line on ADG, then the corresponding effect on FCR of the crossbred is better (worse) than the effect of the V line. The contrasts for FCR₂₈₋₄₂ were significantly positive for all contrasts except HV-VV and LV-VV. On the contrary, the contrasts for FCR₄₂₋₆₃ were always negative and significant with the exception of the contrast where the line A was not involved. As a consequence of the change of sign between both periods, the overall contrasts for FCR₂₈₋₆₃ became non-significant. The confidence intervals at 95% were large for the contrasts between crossbred genetic groups and V line as occurred in the comparison between the lines. This means that relevant differences might exist between the crosses and line V which could not be detected. Thus, the maximum differences, determined by the confidence intervals at 95% would be, 80 g for BW₆₃ (contrast LH-VV), -2.1 g/d for ADG₂₈₋₆₃ (contrast AH-VV), 9 g/d for FI₂₈₋₆₃ (contrast LV-VV) and 0.09 and -0.09 for FCR₂₈₋₆₃ (contrast AH-VV and HV-VV, respectively).

The importance of using a particular line either as sire or dam in a cross was assessed by checking the differences between a particular cross and its reciprocal (Table 6). A given cross and its reciprocal were raised on different farms (Table 1), but connected by line V, which was raised on all the farms. The consequence of this is that the standard

Table 6: Contrasts (standard error) between reciprocal crosses for body weight (¹BW, g), average daily gain (²ADG, g/d), individual feed intake (³FI, g/d) and feed conversion ratio (⁴FCR).

Crosses	AH-HA	AL-LA	AV-VA	HV-VH	LH-HL	LV-VL
BW ₂₈	9(20)	-74(20)*	-16(20)	1(20)	30(20)	-9(20)
BW ₄₂	-31(39)	-56(38)	41(39)	15(38)	17(39)	5(40)
BW ₆₃	-56(52)	-42(52)	21(53)	19(53)	20(53)	7(53)
ADG ₂₈₋₄₂	-1.9(1.6)	-0.7(1.6)	2.0(1.7)	0.5(1.6)	1.3(1.6)	0.1(1.6)
ADG ₄₂₋₆₃	-0.6(1.3)	2.7(1.3)*	-1.2(1.4)	1.0(1.3)	0.1(1.4)	-1.3(1.4)
ADG ₂₈₋₆₃	-1.5(1.1)	1.5(1.1)	0.4(1.1)	0.7(1.1)	0.1(1.1)	-0.3(1.1)
FI ₂₈₋₄₂	5(4)	-1(4)	3(4)	-3(4)	5(4)	2(4)
FI ₄₂₋₆₃	2(6)	0(6)	2(7)	10(6)	5(7)	1(6)
FI ₂₈₋₆₃	3(5)	0(5)	2(5)	5(5)	5(5)	2(5)
FCR ₂₈₋₄₂	0.30(0.08)*	-0.08(0.08)	-0.21(0.08)*	-0.04(0.08)	0.10(0.08)	-0.05(0.08)
FCR ₄₂₋₆₃	0.21(0.12)	-0.14(0.12)	-0.01(0.12)	0.20(0.12)	0.20(0.12)	-0.13(0.12)
FCR ₂₈₋₆₃	0.22(0.07)*	-0.10(0.07)	-0.09(0.07)	0.11(0.07)	0.15(0.07)*	-0.09(0.07)

¹ BW_x, body weight at day x of age. ² ADG_{x-y}, average daily gain between days x and y. ³ FI_{x-y}, individual feed intake between days x and y per day. ⁴ FCR_{x-y}, feed conversion ratio between days x and y. L: LP line. *P < 0.05 (significant difference at $\alpha=0.05$).

errors of the contrasts for the reciprocal effect (Table 6) were higher than for the contrasts between the lines raised on the same farm (Table 4) and for the average of a cross and its reciprocal compared to line V (Table 5). Despite the large standard errors, significant differences for the contrast AL-LA, in favour of LA, were observed for weaning weight (BW₂₈). The effect on pre-weaning growth of the litter size in which one animal was raised could be seen as a maternal effect, which is expected to be under genetic control. The differences in prolificacy might explain the observed effects on reciprocal contrasts. Thus, LA does clearly showed lower prolificacy (10.38 BA and 8.75 NW) than does from the AL cross (11.02 BA and 10.07 NW). It should be noted that the latter showed a significantly higher ADG₄₂₋₆₃ than the LA cross, inverting the sign of the corresponding contrast for ADG₂₈₋₄₂. This could be a manifestation of compensatory growth. It is also important to note that the contrast AH-HA was significant for FCR₂₈₋₄₂ (0.30±0.08) and FCR₂₈₋₆₃ (0.22±0.07), the differences being in favour of that cross in which A line acts as dam and line H as sire. Similarly, the contrast between LH and HL was also favourable for FCR₂₈₋₆₃ (0.15±0.07) to the cross where H line acts as sire. The foundation criteria of the H line based on hyperprolificacy (García-Ximénez *et al.*, 1996) might explain why the H line is preferred to be used as the sire. As a higher prolificacy provides a worse maternal environment, the hyperprolificacy of the H line as dam would penalise body weight, weight gain and feed intake of their progeny (Rouvier *et al.*, 1973; Johnson *et al.*, 1988; Lukefahr *et al.*, 1990; Ferguson *et al.*, 1997). In the contrast between AV and VA for FCR₂₈₋₄₂ a significantly favourable effect (-0.21±0.08) in using the V line as sire was observed, which could also be related to the foundation in the V line, carried out through integrating four populations of high prolificacy. In the significant contrasts for FCR₂₈₋₆₃, given the estimation errors, the maximum values that the 95% confidence interval could reach were 0.36 and 0.29; for those contrasts not showing significant results (HV-VH, AL-LA, AV-VA and LV-VL) the maximum of the differences determined by the confidence interval at 95% could reach values between 0.23 and 0.29, which are quite relevant magnitudes. Ragab (2012) studied the same crosses for reproductive traits and observed no significant differences between reciprocal crosses for the number born alive and weaned. With these results we could use the best reciprocal cross for FCR without impairing reproductive performance of the crossbred females.

So far, the analysis and interpretation of the results have been approached from a productive point of view and a number of contrasts with applied interest has been described; in this context an assessment of the actual economic impact of the observed differences between genetic types is needed. FCR, the second most important trait after the number born alive is followed by: fattening survival, fertility and weaning survival (Cartuche *et al.*, 2013). Cartuche *et al.* (2013) calculated that a reduction of 0.1 in the FCR of the fattening period increases profitability by 2.20 € per

doe. The economic weights of ADG and FI are low, after taking FCR into account. Therefore, in spite of the fact that, in general, no significant differences were observed between lines, either between crosses and the V line, or between reciprocal crosses, for FCR₂₈₋₆₃ the differences could be relevant to this important economic trait.

Direct-maternal effects

Differences between direct-maternal effects are shown in Table 7. At weaning, significant differences for the contrasts G_{A-V}^I and G_{L-V}^I were observed for body weight which agrees with the results obtained in the comparison between lines (Table 4) that revealed that line V was the lightest at weaning. Regarding ADG₂₈₋₄₂ the LP line was significantly superior to the other lines, similarly to the contrasts for all of the effects on the lines as pure dam lines (Table 4). However, this superiority of the LP line was lost during the last 3 wk of the fattening, becoming significantly inferior to the H and V lines for ADG₄₂₋₆₃. The higher direct-maternal effect of the LP line on ADG₂₈₋₄₂ was parallel to a similar effect on FI₂₈₋₄₂. However this parallelism was not evident for the last 3 wk of fattening. Regarding FCR, there were no significant differences during the first 2 wk, despite the differences commented upon for ADG and FI. FCR showed significant differences in the contrasts G_{L-V}^I and G_{A-V}^I , favourable in both cases to the V line. In the contrast G_{L-V}^I significant differences were also observed for the whole of the fattening period. The general positive effect associated with line V on FCR is probably related to the lower body weights of line V as is well known FCR increases with body weight (Torres *et al.*, 1992; Feki *et al.*, 1996; Sánchez *et al.*, 2004).

Throughout the fattening period, in addition to the previously mentioned significant effect for FCR₂₈₋₆₃, significant differences were only observed in BW₆₃ and FI₂₈₋₆₃, also for the contrast G_{L-V}^I , but now favouring LP line. This result partially agrees with results by Mínguez *et al.* (2011), where the LP line was found to be heavier than lines A and V, but not heavier than line H.

The results obtained for A and V lines agree with the results reported by Orengo *et al.* (2009) for BW₆₃, ADG₂₈₋₆₃, FI₂₈₋₆₃ and FCR₂₈₋₆₃, who did not find any relevant difference. The only disagreement with Orengo *et al.* (2009) concerns BW at weaning, in which we observed significant differences, but in their study weaning took place at 32 d instead of 28 d as in ours.

After studying direct-maternal effects (Table 7), as a general result, it can be indicated that V line was the worst in all growth traits. Similar results have been reported when considering the contrast between lines (Table 4). For traits reflecting the complete fattening period, the highest values for the contrast between lines also correspond to the

Table 7: Direct-maternal differences between lines¹ (standard error) for body weight (²BW, g), average daily gain (³ADG, g/d), individual feed intake (⁴FI, g/d) and feed conversion ratio (⁵FCR).

	¹ G_{A-H}^I	G_{A-L}^I	G_{A-V}^I	G_{H-V}^I	G_{L-H}^I	G_{L-V}^I
BW ₂₈	26(23)	-7(18)	41(18)*	14(18)	33(22)	48(17)*
BW ₄₂	-3(43)	-58(33)	61(34)	65(34)	55(43)	120(32)*
BW ₆₃	-54(57)	-56(45)	30(45)	84(45)	2(57)	86(43)*
ADG ₂₈₋₄₂	-0.6(1.8)	-4.1(1.4)*	0.5(1.4)	1.2(1.4)	3.7(1.8)*	4.8(1.4)*
ADG ₄₂₋₆₃	-2.2(1.4)	1.1(1.2)	-1.3(1.2)	0.9(1.2)	-3.3(1.5)*	-2.5(1.1)*
ADG ₂₈₋₆₃	-1.7(1.2)	-1.0(0.9)	-0.5(0.9)	1.2(0.9)	-0.7(1.2)	0.5(0.9)
FI ₂₈₋₄₂	4(5)	-7(4)	4(4)	0(4)	11(5)*	11(3)*
FI ₄₂₋₆₃	-4(7)	-1(6)	8(6)	12(6)*	-3(7)	9(6)
FI ₂₈₋₆₃	0(5)	-3(4)	7(4)	7(4)	3(5)	10(4)*
FCR ₂₈₋₄₂	0.19(0.10)	0.07(0.07)	0.05(0.07)	-0.14(0.08)	0.12(0.09)	-0.02(0.07)
FCR ₄₂₋₆₃	0.14(0.13)	0.02(0.10)	0.25(0.10)*	0.11(0.10)	0.12(0.13)	0.23(0.10)*
FCR ₂₈₋₆₃	0.13(0.08)	0.05(0.06)	0.11(0.06)	0.02(0.06)	0.08(0.08)	0.13(0.06)*

¹ G_{i-j}^I , direct-maternal differences between lines i and j (see text for a complete explanation). ² ADG_{x-y}, average daily gain between days x and y. ³ FI_{x-y}, individual feed intake between days x and y per day. ⁴ FCR_{x-y}, feed conversion ratio between days x and y. L: LP line. *P<0.05 (significant difference at α=0.05).

highest values for the contrast between lines for direct-maternal differences. However, the agreement is not complete because of the importance of the grand-maternal effects of the lines, which will be discussed later, and to the fact that the Dickerson model includes an error that could be important, as in our case. In fact, if the model was perfect, i.e. there was no error, the contrast between lines, for example A and V would be: $AA-VV = G_{A-V}^I + G_{A-V}^M$, according to Table 2.

Grand-maternal effects

Grand-maternal effect differences between lines are shown in Table 8. Comparing the standard errors of the corresponding contrasts for direct-maternal effects (Table 7) and grand-maternal effects it can be observed that the errors for the latter are between 50 and 80% smaller than those for the former, showing that our data structure is better suited to estimate grand-maternal effects than direct-maternal effects. However the number of contrasts found to be significant for grand-maternal effects are fewer than for direct-maternal effects, clearly indicating that the importance of the former should be lower than the importance of the latter.

Significant differences for grand-maternal effects in BW_{28} were not found. The number of weaned is a trait closely related to BW_{28} , for this trait Ragab (2012) did not find any significant difference in maternal genetic effects using the same set of crossbred does. This result is concordant with the absence of significance for BW_{28} observed in our study, thus it can be noted that the dams of the does do not seem to affect litter size at the weaning of their female offspring (maternal effect) or the weaning weight of their grand-progeny (grand-maternal effect). There were significant differences in BW_{42} , favourable to the V line, for the contrasts G_{A-V}^M and G_{L-V}^M , this result is opposite to the estimates obtained for direct-maternal effects. In addition, line V maintained its favourable grand-maternal effect with respect to line LP until the end of fattening (BW_{63}). During the first 2 wk of fattening the effects of line V on ADG as grand-dam were significantly higher than those of the other lines, but during the last 3 wk A line showed a superior effect as grand-dam, and over this period the V line was the worst. Because of the change in the effects between the 2 periods, the contrasts for the whole period were not significant. There were no significant contrasts regarding grand-maternal effects for FI. For FCR contrasts involving V line during the last 3 wk of fattening showed a significant effect against this line. In the first 2 wk the same contrasts showed an opposite sign, being significant for that with the H line. Thus, similarly to what happened with ADG, the contrasts regarding grand-maternal effect for FCR during the 2 periods tended to compensate each other and no significant differences were observed for the whole fattening period (FCR_{28-63}).

Table 8: ¹Grand-maternal differences between lines (standard error) for body weight (²BW, g), average daily gain (³ADG, g/d), individual feed intake (⁴FI, g/d) and feed conversion ratio (⁵FCR).

	¹ G_{A-H}^M	G_{A-L}^M	G_{A-V}^M	G_{H-V}^M	G_{L-H}^M	G_{L-V}^M
BW_{28}	-2(12)	14(14)	-2(16)	1(12)	-16(12)	-16(14)
BW_{42}	-36(23)	-5(26)	-69(30)*	-33(23)	-31(23)	-63(27)*
BW_{63}	-4(31)	52(36)	-21(40)	-17(32)	-56(32)	-73(36)*
ADG_{28-42}	-1.5(1.0)	-1.8(1.1)	-4.2(1.2)*	-2.7(1.0)*	0.3(1.0)	-2.4(1.1)*
ADG_{42-63}	1.9(0.8)*	2.9(0.9)*	3.6(1.0)*	1.7(0.8)*	-1.0(0.8)	0.7(0.9)
ADG_{28-63}	0.7(0.7)	1.2(0.8)	0.3(0.8)	-0.4(0.7)	-0.3(0.7)	-0.9(0.8)
FI_{28-42}	-2(2)	-3(3)	-5(3)	-2(3)	0(3)	-2(3)
FI_{42-63}	-3(4)	2(5)	-6(5)	-2(4)	-6(4)	-8(5)
FI_{28-63}	-3(3)	0(3)	-5(4)	-2(3)	-3(3)	-6(3)
FCR_{28-42}	-0.02(0.05)	0.02(0.06)	0.13(0.07)	0.11(0.05)*	0.00(0.05)	0.10(0.06)
FCR_{42-63}	-0.12(0.07)	-0.09(0.08)	-0.33(0.09)*	-0.20(0.07)*	-0.04(0.07)	-0.24(0.08)*
FCR_{28-63}	-0.05(0.04)	-0.02(0.05)	-0.08(0.05)	-0.03(0.04)	-0.04(0.04)	0.07(0.05)

¹ G_{i-j}^M , grand-maternal differences between lines i and j (see text for a more complete explanation). ² ADG_{x-y} , average daily gain between days x and y. ³ FI_{x-y} , individual feed intake between days x and y per day. ⁴ FCR_{x-y} , feed conversion ratio between days x and y. L: LP line; * $P < 0.05$ (significant difference at $\alpha = 0.05$).

Maternal heterosis.

Estimates of maternal heterosis effects are shown in Table 9. One result which clearly draws attention is that the signs of the majority of the estimates for BW, ADG and FI are negative. This could be a partial consequence of the positive heterosis showed by the crossbred does regarding litter size (Brun and Saleil, 1994; Khalil and Afifi, 2000; Baselga, *et al.* 2003; Brun and Baselga, 2005; Youssef *et al.*, 2008; Ragab, 2012). The higher litter sizes of the crossbred does compared to purebreds would penalise body weight, weight gain and feed intake of their progeny (Rouvier *et al.*, 1973; Johnson *et al.*, 1988; Lukefahr *et al.*, 1990; Ferguson *et al.*, 1997). Regarding this explanation, it is interesting to note that the only estimates involving line A, which is the line with the lowest prolificacy (Ragab and Baselga, 2011), negative and significant effects were obtained for both weight and feed intake traits, whereas in the other cases only weight traits showed significant maternal heterosis effects. The combination of lines A and H is that showing the most important, negative and significant heterosis effects. This result could be related to the low prolificacy of line A, already noted, and with the fact that the cross AH showed a significant positive heterosis for the total born (Ragab, 2012). The estimates of the heterosis for FCR were also negative, particularly for the last part of the fattening, as these were significant for AH and AL, and in this case negative values are favourable. These favourable heterotic effects on FCR at the end of the fattening period are probably related to the negative maternal heterosis on BW63, reduction of slaughter BW in crossbred offspring, which, as already remarked on, reduces FCR (Torres *et al.*, 1992; Feki *et al.*, 1996; Sánchez *et al.*, 2004). Other results that deserve attention are the favourable heterosis effect for ADG₄₂₋₆₃ between lines LP and V, together with the significantly positive and unfavourable heterosis for FCR₂₈₋₄₂ between lines H and V.

In this work, the design of the experiment does not allow the estimation of direct heterosis effects, however this is expected to be of low effect, as this will be a function of non-additive genetic effects which are expected to be irrelevant for the growth traits considered in our study. In fact, the maternal heterosis effects obtained in this study are basically related to the effects of prolificacy on growth, not to growth itself. As a general result it can be indicated that maternal heterosis expressed in percentage was low: inferior or equal to 6%.

Table 9: ¹Maternal heterosis (standard error) for body weight (²BW, g), average daily gain (³ADG, g/d), individual feed intake (⁴FI, g/d) and feed conversion ratio (⁵FCR).

	¹ H _{A-H} ^M	H _{A-L} ^M	H _{A-V} ^M	H _{H-V} ^M	H _{L-H} ^M	H _{L-V} ^M
BW ₂₈	-4(12)	-12(14)	-6(12)	9(10)	20(11)	-17(10)
BW ₄₂	-53(23)*	-62(27)*	-15(23)	-22(20)	-2(22)	-35(19)
BW ₆₃	-35(31)	-31(36)	-32(32)	-24(27)	10(28)	-29(27)
BW ₆₃ ¹ (%)	-2	-1	-1	-1	0	-1
ADG ₂₈₋₄₂	-3.5(1.0)*	-2.9(1.1)*	-0.9(1.0)	-0.8(0.8)	-0.3(0.9)	-1.1(0.8)
ADG ₄₂₋₆₃	1.1(0.8)	1.3(0.9)	-0.0(0.8)	-0.1(0.7)	0.0(0.7)	1.4(0.7)*
ADG ₂₈₋₆₃	-0.7(0.7)	-0.3(0.7)	-0.3(0.7)	-0.7(0.6)	-0.2(0.6)	0.2(0.6)
ADG ₂₈₋₆₃ ¹ (%)	-2	0	-1	-1	0	0
FI ₂₈₋₄₂	-5(2)*	-1(3)	-1(2)	3(2)	2(2)	-2(2)
FI ₄₂₋₆₃	-9(4)*	-6(5)	-5(4)	-5(3)	-6(3)	-5(3)
FI ₂₈₋₆₃	-7(6)*	-4(3)	-3(3)	-2(2)	-4(2)	-4(2)
FI ₂₈₋₆₃ ¹ (%)	-6	-3	-3	-2	-3	-3
FCR ₂₈₋₄₂	0.07(0.05)	0.11(0.06)	0.00(0.05)	0.15(0.04)*	0.03(0.04)	0.04(0.04)
FCR ₄₂₋₆₃	-0.15(0.07)*	-0.23(0.08)*	-0.06(0.07)	-0.03(0.06)	-0.09(0.06)	-0.06(0.06)
FCR ₂₈₋₆₃	-0.04(0.04)	-0.07(0.05)	-0.04(0.04)	0.03(0.04)	-0.04(0.04)	-0.02(0.03)
FCR ₂₈₋₆₃ ¹ (%)	-1	-2	-1	1	-1	0

¹ H_{i-j}^M maternal heterosis between lines i and j; ² ADG_{x-y}, average daily gain between days x and y. ³ FI_{x-y}, individual feed intake between days x and y per day. ⁴ FCR_{x-y}, feed conversion ratio between days x and y. L: LP line. *P<0.05 (significant difference at α=0.05).

CONCLUSIONS

Few significant differences between lines, crosses and V line and reciprocal crosses between them were observed, and in general all of them can be associated with differences in the maternal environments that the different lines and crossbred females are providing to their offspring, either through the size of the litter or the milk production. This lack of significance is a consequence of large errors and not due to an overall lack of effects; the extremes of 95% confidence interval of the contrast effects could reach very relevant values, particularly for FCR during the whole fattening period. After decomposing the estimates of the genetic group effects into direct-maternal, grand-maternal and maternal heterosis effects, following Dickerson's model, similar patterns of effect to those obtained in the comparison between lines and crosses were obtained and negative values of maternal heterosis were observed, which can also be explained by the negative environmental effect that crossbred females provide to their offspring as a consequence of the large litter sizes. In this sense, crossbreeding could be an excellent tool to take advantage of the complementarity between lines to overcome the trade-off between prolificacy and growth performance.

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REFERENCES

- Baselga M. 2004. Genetic improvement of meat rabbits. Programmes and diffusion. In: *Proc. 8th World Rabbit Congress, September 7-10, 2004, Puebla, Mexico*. 1-13.
- Baselga M., Blasco A. 1989. Mejora genética del conejo de producción de carne. *Mundi-Prensa, Madrid, Spain*.
- Baselga M., García M.L., Sánchez J. P., Vicente J. S., Lavara R. 2003. Analysis of reproductive traits in crosses among maternal lines of rabbits. *Anim. Res.*, 52: 473-479. doi:10.1051/animres:2003034
- Belhadi S. 2004. Characterisation of local rabbit performances in Algeria: Environmental variation of litter size and weights. In: *Proc. 8th World Rabbit Congress, September 7-10, 2004, Puebla, Mexico*. 218-223.
- Brun J.M., Saleil G. 1994. Une estimation, en fermes, de l'hétérosis sur les performances de reproduction entre les souches de lapin INRA A2066 et AI077. In: *Proc. 6^{èmes} Journées de Recherche Cunicole, 6-7 Décembre 1994, La Rochelle, France*. 203-210
- Brun J.M., Baselga M. 2005. Analysis of reproductive performances during the formation of a rabbit synthetic strain. *World Rabbit Sci.*, 13: 239-252. doi:10.4995/wrs.2005.514
- Camacho J., Baselga M. 1991. Efectos "no genéticos" directos en la determinación de caracteres productivos en conejos. In: *Proc. IV Jornadas sobre Producción Animal. Zaragoza, Spain*. 210-217.
- Carabaño R. 2000. Sistemas de producción de conejos en condiciones intensivas. In: *Proc. Reunión Anual da Sociedade Brasileira de Zootecnia, Viçosa-MG, Brasil*. 17-38.
- Cartuche L., Pascual M., Gómez E. A., Blasco A. 2013. Estimación de pesos económicos en un sistema de producción de conejos de carne. In: *Proc. 38 Symposium de Cunicultura, May 30-31, 2013, Zamora, Spain*. 8-11
- Cifre P., Baselga M., García-Ximénez F., Vicente J.S. 1998. Performance of hyperprolific rabbit line. I. Litter size traits. *J. Anim. Breed. Genet.*, 115: 131-138. doi:10.1111/j.1439-0388.1998.tb00336.x
- Cifre J., Baselga M., Gómez E.A., García M.L. 1999. Effect of embryo cryopreservation techniques on reproductive and growth traits in rabbits. *Ann. Zootech.*, 48: 15-24. doi:10.1051/animres:19990102
- Dickerson G.E. 1969. Experimental approaches in utilizing breed resources. *Anim. Breed. Abstr.*, 37:191-202.
- El Nagar A.G., Ragab M., Mínguez C., Sánchez J.P., Baselga M. 2013. Comparación de la producción y la composición de la leche en tres líneas maternas de conejo. In: *Proc. XV Jornadas sobre Producción Animal. May 14-15, 2013, Zaragoza, Spain*. 475-477.
- Estany J., Baselga M., Blasco A., Camacho, J. 1989. Mixed model methodology for the estimation of genetic response to selection in litter size of rabbits. *Livest. Prod. Sci.*, 21: 67-75. doi:10.1016/0301-6226(89)90021-3
- Estany J., Camacho J., Baselga M., Blasco A. 1992. Selection response of growth rate in rabbits for meat production. *Génét. Sél. Evol.*, 24: 527-537. doi:10.1186/1297-9686-24-6-527
- Feki S., Baselga M., Blas E., Cervera C., Gómez E.A. 1996. Comparison of growth and feed efficiency among rabbit lines selected for different objectives. *Livest. Prod. Sci.*, 45: 87-92. doi:10.1016/0301-6226(95)00081-X
- Ferguson F.A., Lukefahr S.D., McNitt J.J. 1997. Prewaning variables' influence on market traits in rabbits. *J. Anim. Sci.*, 75: 611-621.
- García-Ximénez F., Vicente J.S., Cifre P., Baselga M. 1996. Foundation of a maternal rabbit line using hysterectomy and embryo cryopreservation. In: *Proc. 6th World Rabbit Congress, July 9-12, 1996, Toulouse, France*. 285-288.
- Johnson Z.B., Harris D.J., Brown C.J. 1988. Genetic analysis of litter size, mortality and growth traits of New Zealand White rabbits. *Prof. Anim. Sci.*, 4: 11-16.
- Khalil M.H., Afifi E.A., Youssef Y.M., Khadr A.F. 1995. Heterosis, maternal and direct genetic effects for litter performance and reproductive intervals in rabbit crosses. *World Rabbit Sci.*, 3: 99-105. doi:10.4995/wrs.1995.247

- Khalil M.H., Afifi E.A. 2000. Heterosis, maternal and direct additive effects for litter performance and postweaning growth in Gabali rabbits and their F1 crosses with New Zealand White. *In: Proc. 7th World Rabbit Congress, 4-7 July 2000, Valencia, Spain.* 431-437.
- Larzul C., Rochambeau H. de. 2004. Comparison of ten rabbit lines of terminal bucks for growth, feed efficiency and carcass traits. *Anim. Res.*, 53: 535-545. doi:10.1051/animres:2004032
- Lukefahr S.D., Cheeke P.R., Patton N.M. 1990. Prediction and causation of litter market traits from preweaning and weaning characteristics in commercial meat rabbits. *J. Anim. Sci.*, 68: 2222-2234.
- MAGRAMA, 2012. Encuesta Nacional de Cunicultura 2008-2009. Available at: http://www.magrama.gob.es/es/estadistica/temas/estadisticas-agrarias/2008_Cunicultura_Memoria_tcm7-14332.pdf Accessed February 2014.
- Medellin M.F, Lukefahr S.D. 2001. Breed and heterotic effects on postweaning traits in Altex and New Zealand White straightbred and crossbred rabbits. *J. Anim. Sci.*, 79: 1173-1178.
- McNitt J.I., Lukefahr S.D. 1990. Effects of breed, parity, day of lactation and number of kits on milk production of rabbits. *J. Anim. Sci.*, 68: 1505-1512.
- Mínguez C. 2011. Comparación de cuatro líneas maternas de conejo en caracteres de crecimiento. *Master Thesis. Polytechnic University of Valencia.*
- Mínguez C., Sánchez J.P., Ragab M., El Nagar A.G., Baselga M. 2012. Growth traits in four maternal lines. *In: Proc 10th World Rabbit Congress, Septiembre 3-6, 2012, Sharm El-Sheikh-Egypt.* 55-59.
- Misztal, I., Tsuruta S., Strabel T., Auvray B., Druet T., Lee D.H. 2002. BLUPF90 and related programs (BGF90). *In: Proc 7th World Congress on Genetics Applied to Livestock Production, August 19-23, 2002, Montpellier, France.* 28-07.
- Morise J.P. 1985. Pathologie digestive: alimentation et zootechnie. *Éleveur de lapins*, 9: 51-55.
- Orongo J., Gómez E.A., Piles M., Ramón J., Rafel O. 2003. Étude des caractères de reproduction en croisement entre trois lignées femelles espagnoles. *In: Proc. 10^{èmes} Journées de la Recherche Cunicole, November 19-20, 2003, Paris, France.* 57-60.
- Orongo J., Gómez E.A., Piles M., Rafel O., Ramon J. 2004. Growth traits in simple crossbreeding among dam and sire lines. *In: Proc. 8th World Rabbit Congress. September 7-10, 2004 Puebla, Mexico.* 114-120.
- Orongo J., Piles M., Rafel O., Ramon J., Gómez E.A. 2009. Crossbreeding parameters for growth and feed consumption traits from a five diallel mating scheme in rabbits. *J. Anim. Sci.* 87: 1896-1905. doi:10.2527/jas.2008-1029
- Ouhayoun J. 1978. Etude comparative de races de lapins différant par le poids adulte. *Doctoral Thesis. Université des Sciences et Techniques du Languedoc.*
- Piles M., Gómez E.A., Rafel O., Ramon J., Blasco A. 2004a. Elliptical selection experiment for the estimation of genetic parameters of the growth rate and feed conversion ratio in rabbits. *J. Anim. Sci.*, 82: 654-660.
- Piles M., Rafel O., Ramon J., Gómez E.A. 2004b. Crossbreeding parameters of some productive traits in meat rabbits. *World Rabbit Sci.*, 12: 139-148. doi:10.4995/wrs.2004.575
- Ragab M. 2012. Genetic analyses of reproductive traits in maternal lines of rabbits and in their diallel cross. *Doctoral Thesis. Polytechnic University of Valencia.*
- Ragab M., Baselga M. 2011. A comparison of reproductive traits of four maternal lines of rabbits selected for litter size at weaning and founded on different criteria. *Livest. Sci.*, 136: 201-206. doi:10.1016/j.livsci.2010.09.009
- Rashwan A.A., Marai I.F.M. 2000. Mortality in young rabbits: A review. *World Rabbit Sci.*, 8: 111-124. doi:10.4995/wrs.2000.427
- Rochambeau H. de. 1988. Genetic of rabbit for wool and meat production. *In: Proc. 4th World Rabbit Congress, October 10-14, 1988, Budapest, Hungary,* 1-68.
- Rouvier R., Poujardieu B., Vrillon J.L. 1973. Statistical analysis of the breeding performances of female rabbits: Environmental factors, correlations, repeatabilities. *Ann. Génét. Sél. Anim.*, 5: 83-107. doi:10.1186/1297-9686-5-1-83
- Sánchez J.P., Baselga M., Silvestre M.A., Sahuquillo J. 2004. Direct and correlated responses to selection for daily gain in rabbits. *In: Proc. 8th World Rabbit Congress. September 7-10, 2004, Puebla, Mexico.* 169-174
- Sánchez J.P., Theilgaard P., Mínguez C., Baselga M. 2008. Constitution and evaluation of a long-lived productive rabbit line. *J. Anim. Sci.*, 86: 515-525. doi:10.2527/jas.2007-0217
- Su G., Kjaer J.B., Brenoe U.T., Sorensen P. 1999. Estimates of genetic parameters in Danish White rabbits using an animal model: I. Growth and carcass traits. *World Rabbit Sci.*, 7: 59-64. doi:10.4995/wrs.1999.381
- Testik A., Baselga M., Yavuz C., García M.L. 1999. Growth performances of California and line V rabbits reared in Turkey. *In: Proc 2nd International Conference on rabbit production in hot climates, Zaragoza, Spain.* 159-162.
- Torres C., Baselga M., Gómez E.A. 1992. Effect of weight daily gain selection on gross feed efficiency in rabbits. *J. Appli. Rabbit Res.*, 15: 884-888.
- Youssef Y.K., Iraqi M.M., El-Raffa A.M., Afifi E.A., Khalil M.H., García M.L., Baselga M. 2008. A joint project to synthesize new lines of rabbits in Egypt and Saudi Arabia: emphasis for results and prospects. *In: Proc. 9th World Rabbit Congress, June 10-13, 2008, Verona, Italy.* p. 1637-1642