Genetic Analyses of Growth, Carcass and Meat Quality Traits in Maternal Lines of Rabbits and Their Diallel Cross

Análisis Genético de Caracteres de Crecimiento, Matadero y Calidad de Carne en Lineas Maternales de Conejo y en su Cruzamiento Dialélico

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By: Carlos Mínguez Balaguer

Valencia, March 2014

The constant is that everybody lies,

The only variable is about what

(M.D. House)

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ABSTRACT

The aim of this thesis was to estimate differences between genetic groups, and estimate crossbreeding parameters for growth, carcass and meat quality traits of rabbits, the dams from which were from full diallel cross among four maternal lines and the sires from a paternal line. The maternal lines were A, V, H and LP, founded for different criteria but all of them selected for litter size at weaning since the foundation until present. For the paternal line, the selection was for postweaning daily gain from 28 to 63 d, and candidates were exclusively evaluated based on their phenotype.

Chapter 1 is a comparison of the maternal lines, at their foundation and at fixed periods of time, for weight at weaning (WW, 28 days), slaughter weight (SW, 63 days) and average daily gain between weaning and slaughter (ADG). Important differences for growth traits were detected between maternal lines at their origin. The H and LP lines were the heaviest. These differences could be partly explained by their different foundation criteria. The procedures for the creation of A and V lines were from New Zealand White and from specialized maternal lines, respectively, while the H and LP were created from crossbred does from meat rabbit commercial populations that could have had some introgression of genes of paternal lines. This would explain the superiority of lines H and LP for growth traits. The comparison of these lines at fixed times allows for the observation of line differences, which were reduced along the generations of selection. This result could have been a consequence of a correlated response on growth after the selection for litter size at weaning, as well as to direct response to a concomitant, non-programmed selection for growth traits, which was

different in intensity between the lines, or also simply as a consequence of genetic drift. These differences show that the processes and criteria followed for the foundation of the lines should be carefully considered, and to base the foundation only on the concept of breed, without considering production criteria does not seem beneficial.

On commercial farms, crossbred does from simple crosses between maternal lines are the most common type of females and, consequently, some differences for growth traits in dam effects might have an economic impact. Chapters 2, 3 and 4 had the objective of evaluating the value of the four maternal lines and their 12 types of crossbred does with regards to growth, carcass and meat characteristics of their three-way crossbred progeny. Crossbreeding parameters were estimated according to Dickerson's model. The averages values for all traits were within the range in the bibliography consulted.

In Chapter 2, genetic group differences and crossbreeding parameters for body weight at weaning (28 days, BW28), body weight at slaughter (at 63 days, BW63), post-weaning average daily gain (ADG), feed intake (FI) and feed conversion ratio (FCR) were measured in 1,955 young rabbits during the complete fattening period. The traits were recorded weekly with the cage being the experimental unit for FI and FCR (283 cages). The rabbits of the sixteen genetic groups were distributed on four Spanish farms and one genetic group (V line) was present on all farms in order to connect records among them and to be used as reference group. Regarding dam effects between purebreds for BW at weaning, A line had the largest effect and showed significant differences with respect to LP and V lines (61 g and 30 g, respectively). During the complete fattening period, the differences favoring A line for BW at weaning were compensated. During the whole fattening period, no significant differences were observed between the lines. At the end of the fattening period, no significant differences

were observed between the crossbred groups. Regarding the reciprocal effects, the most important results were the significant effects for FCR favoring H line as sire in HA and HL (AH-HA=0.22 and LH-HL=0.15, respectively). The estimates of maternal heterosis were, in general, negative. This could be a consequence of positive heterosis for litter size, but the analysis using number born alive as covariate did not confirm this hypothesis. The combination of direct and maternal effects of the V line was poorest for all growth traits showing significant differences with the LP line for most of them, for instance 0.13 was poorest for FCR between 28 and 63 d. Grand-maternal effects were less important than direct-maternal effects.

In Chapter 3, the genetic group effects and the crossbreeding genetic parameters of slaughter and carcass traits were estimated using carcass parts of the rabbits from work reported in Chapter 2. The slaughter traits recorded were live weight at 63 days (day of slaughter), commercial skin weight, full gastrointestinal tract weight, hot carcass weight, and dressing percentage. After slaughtering, the carcasses were stored at 4º C for 24 hours. The carcass traits studied were carcass colour, commercial carcass weight, head weight, liver weight, kidneys weight, thoracic viscera weight, reference carcasses weight, scapular carcass weight, perirenal fat weight, hind leg weight, loin weight, fore leg weight, thoracic cage weight and meat bone ratio. A and LP lines had the smallest effects for dressing percentage (-1.71 and -1.98 compared with H line and -1.49 and -1.75 with the V line, respectively). A line had the strongest effect on commercial carcass weight (83 g more than H line and 60 g more than V line). The differences between purebred animals on dressing percentage were transferred to crossbred groups although their magnitude was lower than in purebred lines. For the rest of traits studied, no significant differences were observed between the crossbred groups and between reciprocal crosses. Grand-maternal effects were of lower magnitude and with opposite

signs to the direct-maternal effects. The estimates of maternal heterosis were, in general, negative. This result was previously discussed for the growth traits, which again could have been a consequence of positive heterosis for litter size but, again, the inclusion of number born alive into the models did not support this hypothesis.

Chapter 4 of this thesis dealt with meat quality traits. These traits were pH, colour, intramuscular fat (IMF), protein, fatty acid groups (SFA, MUFA, PUFA, n-3PUFA and n-6PUFA), fatty acid ratios (n-6/n-3 and PUFA/SFA) and the individual fatty acids. The pH and meat colour were measured in 950 *Longissimus* muscles (LM) which were excised from carcasses used in Chapter 3. The rest of the meat quality traits were recorded by NIRS from a sample of 285 LM that were previously used. For pH, A line showed a 0.05 higher unit advantage than LP line, although this difference was significant but not relevant. No differences in protein were found. The line A had significant differences over the the V line for IMF, SFA, MUFA, PUFA, n-3PUFA and n-6PUFA of 230, 67, 66, 34, 3.1 and 25 (mg/100 g of muscle), respectively, and for the majority of individual fatty acids. Regarding the comparisons between the crosses and V line, the effect of the crossbred AH was superior for IMF, SFA, MUFA, PUFA, n-3PUFA, n-6PUFA and for some of individual fatty acids. No significant differences were found for other contrasts, although it seems that crossbreds involving A line tended to have higher content for IMF and fatty acids groups. No significant differences were found for the contrasts All-V. In general, the reciprocal cross effects were not significant. With regards to crossbreeding parameters, there were significant differences between A and LP lines in direct-maternal effects for pH (0.08) and between A and V for IMF, SFA, MUFA, PUFA, n-3PUFA and n-6PUFA of 200, 63, 61, 33, 2.9 and 31 mg/100g, respectively, in favor of the A line. No significant differences were found for the grand-maternal effects, and in general were of lower magnitude than the

direct-maternal effects. No significant values of maternal heterosis were found, being explained by the relative independence of meat quality traits from litter size.

RESUMEN

El principal objetivo de esta tesis fue estimar diferencias entre grupos genéticos y parámetros de cruzamiento para caracteres de crecimiento, canal y calidad de carne en conejos. Sus madres provienen de un cruce dialélico completo entre cuatro líneas maternales y los padres de una línea paternal. Las líneas maternales fueron la A, V, H y LP, fundadas por diferentes criterios, pero todas ellas seleccionadas por tamaño de camada al destete. La selección para la línea paternal (línea R) se realiza por ganancia diaria post-destete entre los 28 hasta los 63 d.

En el Capítulo 1, se realizó una comparación entre las líneas maternales en su fundación y en periodos de tiempos fijos, para los caracteres de peso al destete (WW, 28 días), peso al sacrificio (SW, 63 días) y ganancia media diaria entre el destete y el sacrificio (ADG). Se encontraron importantes diferencias para los caracteres de crecimiento entre las líneas en el origen. Las líneas H y LP fueron las de mayor peso. Sus diferencias podrían parcialmente ser explicadas en función de los diferentes criterios de fundación, ya que las líneas H y LP se crearon a partir de conejas cruzadas procedentes de poblaciones comerciales, en las cuales podría haber introgresión de genes de líneas paternales. La comparación de estas líneas en periodos fijos permitió observar que las diferencias observadas en el origen de las líneas se reducían a través de las generaciones de selección. Esto podría ser la respuesta correlacionada en los

caracteres de crecimiento al seleccionar por tamaño de camada al destete, la respuesta directa a una selección concomitante y no programada para estos caracteres de crecimiento, el resultado de la deriva genética o una combinación de los anteriores. Estas diferencias muestran que el proceso y criterio seguido para la fundación de una línea debe ser cuidadosamente considerado.

En las granjas comerciales, las conejas cruzadas procedentes de cruces simples entre líneas maternales son las más comunes, y consecuentemente, algunas diferencias en caracteres de crecimiento podrían tener un impacto económico importante. Los Capítulos 2, 3 y 4 tuvieron el objetivo de evaluar las hembras de las cuatro líneas maternales y sus 12 tipos de cruces simples (16 grupos genéticos) para los caracteres de crecimiento, canal y calidad de carne. Los caracteres se midieron en la progenie de las hembras anteriores cruzadas con machos de la línea paternal. Los parámetros de cruzamiento se estimaron de acuerdo con el modelo de Dickerson. Los valores medios para todos los caracteres medidos estaban dentro de la bibliografía consultada.

En el Capítulo 2, los caracteres peso al destete (28 días, BW_{28}), peso al sacrificio (63 días, BW_{63}), ganancia media diaria (ADG), consumo diario (FI) e índice de conversión (FCR) fueron medidos en 1,995 gazapos durante el periodo completo de cebo. Los datos fueron recogidos semanalmente, siendo la jaula la unidad experimental para FI y FCR (283 jaulas). Los dieciséis grupos genéticos fueron distribuidos en cuatro granjas, y un grupo genético (línea V) estuvo presente en todas las granjas para conectar los datos entre ellas y ser usado como grupo de referencia. Respecto a BW_{28}, la línea A mostró diferencias significativas en relación a las líneas LP y V (61, y 30 g, respectivamente). En el periodo completo de cebo, las diferencias a favor de la línea A para BW_{28} se compensaron. Tampoco se observaron diferencias significativas entre los diferentes cruces para el periodo completo de cebo. En la comparación entre cruces recíprocos, el

resultado más importante fue para el carácter FCR a favor de la línea H como macho en los cruces HA y HL (AH-HA = 0.22 y LH-HL = 0.15, respectivamente). Las estimas de la heterosis materna fueron, en general, negativas. Esto podría ser consecuencia de la heterosis positiva para el carácter de tamaño de camada, si bien esta hipótesis no resultó confirmada cuando el número de nacidos vivos era utilizado como covariable. En relación a los efectos directo-maternos, la línea V fue la peor para los caracteres de crecimiento, mostrado diferencias significativas con la línea LP para casi todos ellos. Los efectos de abuela fueron menos importantes que los efectos directo-maternos.

En el Capítulo 3, las diferencias entre grupos genéticos y parámetros de cruzamiento para caracteres de canal y matadero se estimaron usando una muestra aleatoria de las canales de los conejos utilizados en el Capítulo 2. Los caracteres de matadero medidos fueron peso vivo al sacrificio (63 días), peso de la piel, peso de tracto intestinal, peso de la canal caliente y rendimiento. Después del sacrificio, las canales se almacenaron a 4º C durante 24 horas. Los caracteres de canal estudiados fueron el color de la canal, peso de la canal comercial, peso de la cabeza, peso del hígado, peso de los riñones, peso de las vísceras torácicas, peso de la canal de referencia, peso de la grasa escapular, peso de la grasa peri renal, peso de las patas posteriores, peso de los lomos, peso de las patas anteriores, peso de la caja torácica y el ratio músculo/hueso. Las líneas A y LP mostraron el menor efecto para el rendimiento (-1.71 y -1.98 comparadas con la línea H y de -1.49 y -1.75 con la línea V, respectivamente). La línea A mostró el mayor efecto en el peso de la canal comercial (83 g más que la línea H y 60 g más que la V). Las diferencias entre líneas para rendimiento, se observaron en los cruces pero con menor magnitud. Para el resto de caracteres estudiados, no se observaron diferencias significativas ni entre cruces ni entre cruces recíprocos. Las estimas de la heterosis maternal fueron, en general, negativas. Este resultado fue previamente discutido para los

caracteres de crecimiento, podría ser una consecuencia de la heterosis positiva para el tamaño de camada pero tampoco fue confirmado cuando el número de nacidos vivos se utilizó como covariable.

En el Capítulo 4 se estudiaron los caracteres de calidad de carne. Estos caracteres fueron pH, color, grasa intramuscular (IMF), proteína, grupo de ácidos grasos (SFA, MUFA, PUFA, n-3PUFA y n-6PUFA), ratio de ácidos grasos (n-6/n-3 y PUFA/MUFA) y los ácidos grasos individuales. El pH y el color de la carne fueron medidos en 950 músculos *Longissimus* (LM) que procedían de las canales usadas en el Capítulo 3. El resto de caracteres se midieron por NIRS sobre una muestra de 285 LM provenientes de los LM anteriores. Para el pH, la línea A mostró una diferencia significativa con respecto a la línea LP (0.05), aunque esta diferencia no es relevante. No se observaron diferencias en contenido de proteína. La línea A tuvo diferencias significativas con respecto a la línea V para IMF, SFA, MUFA, PUFA, n-3PUFA, n-6PUFA de 230, 67, 66, 34, 3.1 y 25 (mg/100 g de músculo) respectivamente, y para la mayoría de ácidos grasos individuales. Con respecto a la comparación entre cruces, el cruce AH se mostró superior a la línea V para IMG, SFA, MUFA, PUFA, n-3PUFA, n-6PUFA y para algunos ácidos grasos individuales. No se encontraron diferencias significativas para los demás contrastes, aunque parecía que los cruces en que la línea A estaba involucrada tendían a tener mayor contenido de IMF y el grupo de ácidos grasos. En general, en los cruces recíprocos no se obtuvieron diferencias significativas. Con respecto a los parámetros de cruzamiento, hubieron diferencias significativas entre las líneas A y LP en los efectos directos-maternos para pH (0.08) y entre las líneas A y V para IMF, SFA, MUFA, PUFA, n-3PUFA y n-6PUFA de 200, 63, 61, 33, 2.9 y 31 (mg/ 100 g de músculo), respectivamente, a favor de la línea A. No se encontraron diferencias para los efectos abuela. No se observaron diferencias significativas para la heterosis materna, y

se acepta una independencia relativa entre los caracteres de calidad de carne y el tamaño decamada.

RESUM

El principal objectiu d'aquesta tesi fou estimar diferències entre grups genètics i paràmetres de creuament per a caràcters de creixement, canal i qualitat de la carn en conills. Les seues mares provenien d'un creuament dialélic complet entre quatre línies maternals i els pares d'una línia paternal. Les línies maternals van ser la A, V, H i LP, fundades per diferents criteris, però totes elles seleccionades per grandària de ventrada al deslletament. La selecció per a la línia paternal (línia R) es realitza per líncrement diari post-deslletament entre els 28 fins als 63 dies.

En el Capítol 1, es va realitzar una comparació entre les línies maternals en la seua fundació i en períodes de temps fixos, per als caràcters de pes al deslletament (WW, 28 dies) , pes al sacrifici (SW, 63 dies) i increment mitjà diàri entre el deslletament i el sacrifici (ADG) . Es trobaren importants diferències per als caràcters de creixement entre les línies a l'origen. Les línies H i LP van ser les de major pes que podrien ser explicades en funció dels diferents criteris de fundació, ja que les línies H i LP es van crear a partir de conilles creuades procedents de poblacions comercials, en les quals podria haver-hi introgressió de gens de línies paternals. La comparació d'aquestes línies en períodes fixos va permetre observar que les diferències observades en l'origen de les línies es reduïen a través de les generacions de selecció. Açò podria ser la resposta correlacionada en els caràcters de creixement al seleccionar per grandària de ventrada al deslletament, la resposta directa a una selecció concomitant i no programada per

aquestos caràcters de creixement, el resultat de la deriva genètica o una combinació dels anteriors. Aquestes diferències mostren que el procés i criteri seguit per a la fundació d'una línia ha de ser cuidadosament considerat.

A les granges comercials, les conilles creuades procedents d'encreuaments simples entre línies maternals són les més comunes, i conseqüentment, algunes diferències en caràcters de creixement podrien tindre un impacte econòmic important. Els Capítols 2, 3 i 4 van tindre l'objectiu d'avaluar les femelles de les quatre línies maternals i els seus 12 tipus de creuaments simples (16 grups genètics) per als caràcters de creixement, canal i qualitat de la carn. Els caràcters es van mesurar en la progènie de les femelles anteriors creuades amb mascles de la línia paternal. Els paràmetres de creuament es van estimar d'acord amb el model de Dickerson. Els valors mitjans per a tots els caràcters mesurats estaven dins de la bibliografia consultada.

Al Capítol 2, els caràcters pes al deslletament (28 dies, BW28) , pes al sacrifici (63 dies, BW63), increment mitjà diari (ADG), consum diari (FI) i índex de conversió (FCR) van ser mesurats en 1,995 conills durant el període complet d'abast. Les dades van ser arreplegats setmanalment, la gàbia fou la unitat experimental per a FI i FCR (283 gàbies) . Els 16 grups genètics van ser distribuïts en quatre granges, i un grup genètic (línia V) va estar present en totes les granges per a connectar les dades entre elles i ser usat com a grup de referència. Respecte a BW28, la línia A va mostrar diferències significatives en relació a les línies LP i V (61, i 30 g, respectivament) . Al període complet d'abast, les diferències a favor de la línia A per a BW28 es van compensar. Tampoc van ser observades diferències significatives entre els diferents creuaments per al període complet d'abast. En la comparació entre creuaments recíprocs, el resultat més important va ser per al caràcter FCR a favor de la línia H com a mascle en els creuaments HA i HL (AH-HA = 0.22 i LH-HL = 0.15, respectivament).

Les estimes de l'heterosis materna van ser, en general, negatives. Açò podria ser conseqüència de l'heterosis positiva per al caràcter de grandària de ventrada, si bé aquesta hipòtesi no va resultar confirmada quan el número de nascuts vius era utilitzat com covariable. En relació als efectes directe-materns, la línia V va ser la pitjor per als caràcters de creixement, mostrat diferències significatives amb la línia LP per a quasi tots ells. Els efectes de iaia van ser menys importants que els efectes directe-materns.

Al Capítol 3, les diferències entre grups genètics i paràmetres de creuament per a caràcters de canal i escorxador es van estimar usant una mostra aleatòria de les canals dels conills utilitzats en el Capítol 2. Els caràcters d'escorxador mesurats van ser pes viu al sacrifici (63 dies), pes de la pell, pes de tracte intestinal, pes de la canal calenta i rendiment. Després del sacrifici, les canals es van emmagatzemar a 4º C durant 24 hores. Els caràcters de canal estudiats van ser el color de la canal, pes de la canal comercial, pes del cap, pes del fetge, pes dels renyons, pes de les vísceres toràciques, pes de la canal de referència, pes del greix escapular, pes del greix peri renal, pes de les potes posteriors, pes dels lloms, pes de les potes anteriors, pes de la caixa toràcica i el ràtio múscul/so. Les línies A i LP van mostrar el menor efecte per al rendiment (-1.71 i -1.98 comparades amb la línia H i de -1.49 i -1.75 amb la línia V, respectivament) . La línia A va mostrar el major efecte en el pes de la canal comercial (83 g més que la línia H i 60 g més que la V) . Les diferències entre línies per a rendiment, es van observar en els creuaments però amb menor magnitud. Per a la resta de caràcters estudiats, no es van observar diferències significatives ni entre creuaments ni entre creuaments recíprocs. Les estimes de l'heterosis maternal van ser, en general, negatives. Aquest resultat va ser prèviament discutit per als caràcters de creixement, podria ser una conseqüència de l'heterosis positiva per a la grandària de ventrada però tampoc va ser confirmat quan el número de nascuts vius es va utilitzar com covariable.

Al Capítol 4 es van estudiar els caràcters de qualitat de carn. Aquestos caràcters van ser pH, color, greix intramuscular (IMF) , proteïna, grup d'àcids grassos (SFA, MUFA, PUFA, n-3PUFA i n-6PUFA) , ràtio d'àcids grassos (n-6/n-3 i PUFA/MUFA) i els àcids grassos individuals. El pH i el color de la carn van ser mesurats en 950 músculs Longissimus (LM) que procedien de les canals usades en el Capítol 3. La resta de caràcters es van mesurar per NIRS sobre una mostra de 285 LM provinents dels LM anteriors. Per al pH, la línia A va mostrar una diferència significativa respecte a la línia LP (0.05) , encara que aquesta diferència no és rellevant. No es van observar diferències en contingut de proteïna. La línia A va tindre diferències significatives respecte a la línia V per a IMF, SFA, MUFA, PUFA, n-3PUFA, n-6PUFA de 230, 67, 66, 34, 3.1 i 25 (mg/100 g de múscul) respectivament, i per a la majoria d'àcids grassos individuals. Respecte a la comparació entre creuaments, el creuament AH es va mostrar superior a la línia V per a IMG, SFA, MUFA, PUFA, n-3PUFA, n-6PUFA i per a alguns àcids grassos individuals. No es van trobar diferències significatives per als altres contrastos, encara que pareixia que els creuaments en què la línia A estava involucrada tendien a tindre major contingut d'IMF i el grup d'àcids grassos. En general, en els creuaments recíprocs no es van obtindre diferències significatives. Respecte als paràmetres de cruament, van haver-hi diferències significatives entre les línies A i LP en els efectes directes-materns per a pH (0.08) i entre les línies A i V per a IMF, SFA, MUFA, PUFA, n-3PUFA i n-6PUFA de 200, 63, 61, 33, 2.9 i 31 (mg/ 100 g de múscul), respectivament, a favor de la línia A. No es van trobar diferències per als efectes iaia. No es van observar diferències significatives per a l'heterosis materna, i s'accepta una independència relativa entre els caràcters de qualitat de carn i la grandària de ventrada.

CHAPTER 1. LITERATURE REVIEW

1.1 CROSSBREEDING.

Crossbreeding, is a way to increase production, which combines differences between lines or breeds of interest to create new breeds (Rhoad, 1949; Porter, 1993) or lines (Gregory et al., 1991; Youssef et al., 2008), or to perform regular crosses that take advantage of the complementarity and heterosis effects between the lines or breeds in the cross. The complementarity refers to the fact that, depending on the trait considered, one line or other can be the best performing, and consequently it depends on the genotypic value of the lines for the traits. The heterosis or hybrid vigor, for a given trait and couple of lines represents the difference between the value of the trait in the F_1 obtained from crossing the two lines, and the average of the values of the parental lines. The genetic basis of the heterosis is dominance, epistasis and allele frequency differences between lines. The simplest model, and perhaps the most common, relies on the dominance effects (Parson and Bodmer, 1961; Falconer and Mackay, 1996), and some of the models (that will be presented later) used to estimate heterosis and other crossbreeding parameters, assume that dominance is the principal genetic effect considered. Because the additive effects do not produce heterosis, the importance of the heterosis is generally lower in traits with high heritabilities than in others with low

heritabilities. This means that it is expected that heterosis will be more important in traits related with reproduction than in traits related to growth or carcass and meat quality.

For some traits for which the maternal effects have to be considered, it is necessary to distinguish between individual and maternal heterosis. In animal production, different types of regular crosses have been used to take advantage of the complementarity, individual heterosis or maternal heterosis between the available lines or breeds involved in the cross. Next, a short description of the most common types of regular crosses is made, noting the importance of the complementarity or the heterosis in each of them.

The most simple cross (Figure 1), that produce a F_1 between two lines, being relatively common in sheep and cattle, allows for the use of the complementarity between the two lines and their individual heterosis.

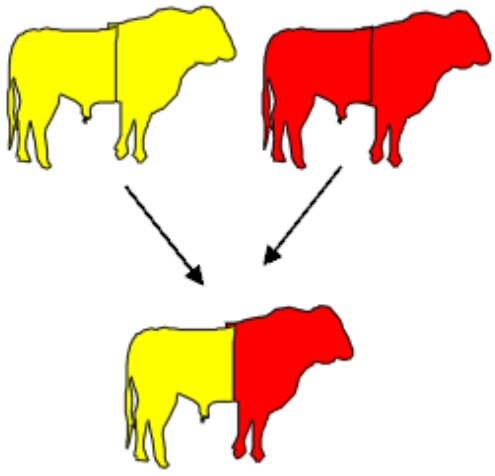

Figure 1. Simple cross

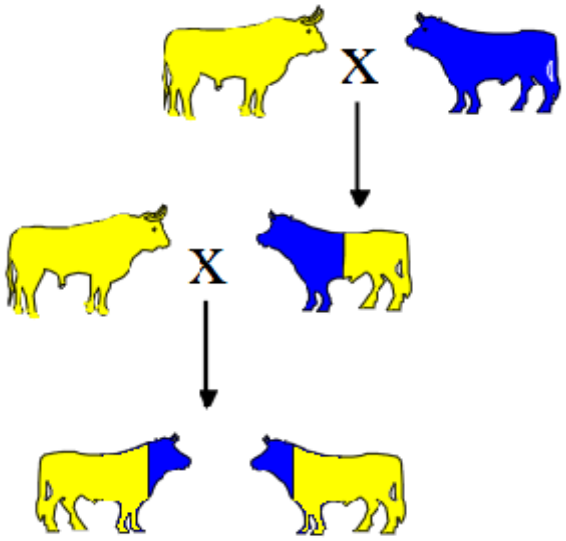

Figure 2. Backcross

A backcross is obtained when the F_1, commonly the female parent, is mated to one of the paternal lines (Figure 2). Thus, when only two parental breeds are available, it is possible to exploit the complementarity, the maternal heterosis in the female F_1 and half the individual heterosis in the backcrossed progeny.

In prolific species, the three-way cross or double-cross (Figure 3) is the most commonly used system that allows for a more complete and flexible use of the complementarity, individual heterosis and maternal heterosis. The crossbred dams take advantage of the complementarity and individual heterosis of the first two lines or breeds and the final product exploits individual heterosis between the third line or breed and the first two, the maternal heterosis between the first two and the complementarity between the three, especially between the third line or breed and the others. The third line or breed, that usually is the sire of the final product, is commonly chosen because of its good or extreme characteristics of growth, conformation or quantity of lean.

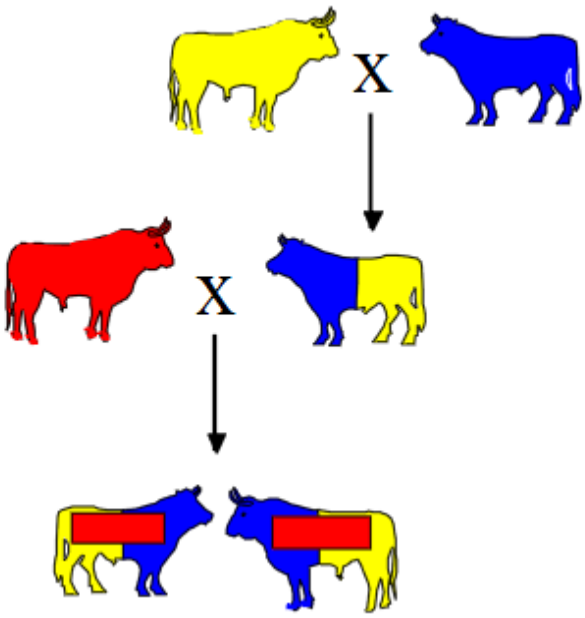

Figure 3. Three-way cross

Other types of crosses are the four-way crosses and the rotational crosses. The first is used when there are commercial, biological or commercial reasons to use crossbred sires (F_1) and crossbred dams (F_1) of the final product. To have an extra line or breed to produce crossbred sires is not always economically justified. The rotational crosses, involving two or more lines or breeds, have an interest in species of low prolificacy to solve the problems in producing female replacements although losing some of the heterosis. In this type of cross, the female replacement, in successive generations, comes from the last cross. The males used as sires in a given generation belong to only one of the lines or breeds, following a sequential order or rotation along the generations.

1.2 CROSSBREEDING EFFECTS.

The value of a set of crosses can be interpreted as a combination of effects, called crossbreeding effects that in turn can be used to predict the expected values of other

crosses involving the same lines. When n lines participate in the crosses, the number of effects that take into account the simple effects and all possible interactions between them is n(2n-1), but the number of effects that can be estimated is either equal or lower than the types of crosses evaluated. It means that the estimation of all effects, when for example four lines participate in the crosses, needs the evaluation of 28 different types of crosses (Wolf et al., 1995); this task is completely unaffordable. Different models have been developed to face this problem, limiting the parameters considered. For instance, Kinghorn (1987) proposed models with only one epistatic effect, independent of the number of lines considered. However, Eberhart and Gardner (1966) and Dickerson (1969) proposed models with one epistatic effect for each couple of lines. Wolf et al. (1995) proposed models that take into account interactions of second and higher orders, showing the equivalence between parameters of the different models as reparametrization of a general model that considers the complete set of parameters. In the following, addressed will be the way that different estimable effects are parameterized when the genetic types evaluated are: a) pure lines and the simple crosses between them or b) some or all of the types in a) and other more complex crosses.

1.2.1 Diallel cross.

A complete diallel cross between n lines, is defined as the set of n^2 genetic types comprising the n pure lines and the n(n-1) simple crosses between them, that includes each cross and its reciprocal. If the lines involved can be considered as lines with a coefficient of inbreeding F, randomly derived from a panmictic base population, the crossbreeding effects and the variance associated can be related to the variance of the different types of genetic effects in the base population (Griffing, 1956). In the case of a diallel cross, the concepts of general combining ability (GCA) and specific combining

ability (SCA) are useful to define a simple model to explain the genotypic values of the genetic types considered.

The definitions of GCA and SCA were introduced by Sprague and Tatum (1942) in a study of corn. The GCA of a line i (GCA_i) is the difference of the average of the genetic values of the crosses in which the line participates and the overall mean (μ) in the diallel cross. Similarly, the SCA between the lines i and j (SCA_{ij}) is defined as the difference of the genetic value of the cross between the lines (Y_{ij}) to the overall mean and the corresponding general combining abilities.

Thus, the model to explain the genetic values of the crosses, in a model without maternal effects, can be written as:

$$G_{ij} = \mu + GCA_i + GCA_j + SCA_{ij} \qquad (1)$$

The GCA is due to the genetic additive effects and to the epistatic effects that include only additive combinations. The SCA depends on the dominance effects and the epistatic effects that include dominance combinations. From a statistical point of view, the GCA is a principal or main effect, and the SCA is an interaction effect.

It is possible to compute the variance between crosses, σ^2_G, as the covariance between the values of the trait among two animals pertaining to the same cross. Taking into account that the coefficient of relationship between the two individuals is F/2 and the coefficient of identity F^2:

$$\sigma_G^2 = F\sigma_A^2 + F^2\sigma_D^2 + F^2\sigma_{AA}^2 + F^3\sigma_{AD}^2 + F^4\sigma_{DD}^2 + ... (2)$$

The part of σ_Y^2 that includes the additive effects and the epistatic effects without dominance combinations corresponds to the variance of the GCA (σ_{GCA}^2**)**, and the rest to the variance of the SCA (σ_{SCA}^2**).** Then,

$$\sigma_{GCA}^2 = F\sigma_A^2 + F^2\sigma_{AA}^2 + F^3\sigma_{AAA}^2 + ... \quad (3)$$

and,

$$\sigma_{SCA}^2 = F^2\sigma_D^2 + F^3\sigma_{AD}^2 + F^4\sigma_{DD}^2 + ... \quad (4)$$

Henderson (1952) extended the model taking into account the maternal effects of the lines.

When the lines involved in a diallel cross cannot be considered as derived from a panmictic base population by a regular process of increasing the inbreeding, the concepts of GCA, SCA and the corresponding variances cannot be related to parameters of the common base population, having meaning for other lines derived from the same process. In this case, Gardner and Eberhart (1966) proposed a model that formally is identical to the model presented above, but with a notation and meaning restricted to the lines participating in the diallel cross. The notation of the model would be:

$$G_{ij} = h + h_i + h_j + s_{ij} \quad (5)$$

where:

h = average heterotic effect.

h_i = heterotic effect of the line i.

s_{ij} = specific heterosis between lines i and j.

Dickerson (1993), Ghosh and Das (2004) and Lessa de Assis and Carneiro (2004) agree that the diallel cross is an effective method to evaluate the genetic and heterotic potential of the breeds or lines involved in genetic programs.

A complete diallel cross experiment can be unfeasible in practice if the number of lines to compare is relatively high. As mentioned before, the n pure lines correspond to n(n-1) simple crosses.

1.2.2 Other type of crosses.

Here, we are dealing with the situation of parametrizing of the estimable crossbreeding effects when the genetic types evaluated involve some pure lines, some simple crosses between pure lines and more complex crosses, as F_2, backcrosses, crosses involving more than two lines or other types. It has been previously mentioned that several models has been proposed to deal with this situation (Eberhart and Gardner, 1966; Dickerson, 1969; Kinghorn, 1987; Wolf et al., 1995). Next, the model of Dickerson (1969) is presented because of its relative simplicity and common use to analyze crossbreeding experiments in animal production. In this model the effects considered are the ones related to the lines themselves (additive effects of the lines, g_j for the line j), the so-called heterosis between two lines (h_{ij} between lines i and j**)** and the recombination loss between two lines (r_{ij}). When maternal effects are relevant for the analyzed traits , the model considers the effects mentioned before as attributed to the genotype of the individuals (I) of the crosses (g_j^I , h_{ij}^I and r_{ij}^I) and to the genotype of the

dams (M) of the individuals of the crosses (g_j^M , h_{ij}^M and r_{ij}^M). Thus, the model for an experiment involving n lines can be written as:

$$G_C = \mu + \sum_{j=1}^{n} \alpha_j g_j^I + \sum_{k=1}^{n} \beta_k g_k^M + \sum_{l \neq m} \gamma_{lm} h_{lm}^I + \sum_{r \neq p} \delta_{rp} h_{rp}^M + \sum_{l \neq m} \varepsilon_{lm} r_{lm}^I + \sum_{r \neq p} \lambda_{rp} r_{rp}^M \quad (6)$$

where, α_j (β_j) is the contribution of line j (k) to the genotype of the individuals (dams) of the cross C; γ_{ij} (δ_{ij}) is the probability that at a given locus of one individual (dam) of the cross C, one gene derived from the line i and the other of the line j; the coefficient ε_{ij} (λ_{ij}) is related to the probability of recombination between genes of the line i and j in the gametes that produced the individuals (dams) of the cross C.

According to the definitions given above for the coefficients, the following conditions must be held:

$$\sum_{j=1}^{n} \alpha_j = 1;\ \sum_{k=1}^{n} \beta_k = 1; \sum_{l \neq m} \gamma_{lm} \leq 1; \sum_{l \neq m} \delta_{lm} \leq 1;\ \sum_{l \neq m} \varepsilon_{lm} < 1; \text{ and } \sum_{l \neq m} \lambda_{lm} < 1 \quad (7)$$

For example, in a tree-way cross between a purebred line sire (R) and a F_1 dam (AxV), the interpretation would be as follows:

$$G_{Rx(AxV)} = \mu + \frac{1}{4} g_A^I + \frac{1}{4} g_V^I + \frac{1}{2} g_R^I + \frac{1}{2} g_A^M + \frac{1}{2} g_V^M + \frac{1}{2} g_V^{M'} + \frac{1}{2} h_{RA}^I + \frac{1}{2} h_{RV}^I + h_{AV}^M + \frac{1}{2} r_{AV}^I \quad (8)$$

In this example, a new effect, $g_V^{M'}$, has been introduced. It corresponds to the contribution of the line V to the genotype of the maternal granddam of the cross.

The "recombination losses" used in the model of Dickerson try to take into account the observation that in some cases the heterosis observed in the F_2 is lower than half the heterosis observed in the F_1 (Sheridan, 1981). These losses are interpreted as losses of

some “favorable” epistatic combinations present in the parental populations when the gametes contributing to the F2 are formed. The term “recombination loss” can cause some confusion when the estimates are positive. Despite the simplicity of the model presented, when the maternal effects are also considered the number of effects estimated are too large. In this case, a common strategy is to not include the recombination losses because they are terms that theoretically are not needed for traits in which the dominance is important and the epistasis negligible (Hill, 1982).

The analysis of the data of an experiment of crossbreeding allows for the computation of estimable functions of the performances of the different genetic groups involved and the corresponding variance-covariance matrix of their errors. The previous estimable functions can be expressed as linear combinations of some functions of the Dickerson parameters that can be estimated using a generalized least square approach (Baselga et al., 2003).

1.3 CROSSBREEDING FOR GROWTH, CARCASS AND MEAT QUALITY IN FARM ANIMALS.

The meat industry competes for consumers who have many choices of high quality meats. To compete effectively, the industry needs to produce uniform, nutritious, lean meat that satisfies the eating preferences of consumers and to improve reproductive efficiency and reduce labor requirements so that seedstock and commercial herds are both practical and profitable under a range of production environments. Thus, the efficiency of meat production is usually maximized in terminal crossbreeding systems by the use of specialized paternal breeds or lines for growth and carcass traits to complement maternal characteristics of dams.

Several types of crossbreeding systems have been developed in domestics animals. This review attempts to explain some examples of crossbreeds made in practice in the most important farm animal species. This literature review is focused on the use of a final or terminal line or breed selected for growth, carcass or meat quality traits.

1.3.1 Beef cattle.

Today, two of the main interests in crossbreeding in beef cattle are focused on the improvement of marbling and the adaptation to subtropical regions.

Carcass marbling is a characteristic that determines the price of beef in the Japanese beef market (Baud et al., 1998). The Japanese government also has interest in exporting beef from developed countries to Japan (Hirooka et al., 1996). Consequently, marbling is an economically important trait for international and domestic markets.

Thus, there has been increased interest in evaluating growth and carcass characteristics using Japanese genetic material (Lunt et al., 1993; Wheeler et al., 2004).

Casas et al. (2006) showed that Hereford, Angus and Scandinavian breeds crossed with traditional Japanese breeds as Japanese Black and Japanese Red had calves with poorer values for growth and carcass composition traits that beef breeds traditionally used. The poorer values for growth and carcass composition in the crosses with Japanese breeds are in agreement with Wheeler et al. (2004), Kuber et al. (2004), Pitchford et al. (2002), Mears et al. (2001) and Mir et al. (1999). With these results, the producer needs to know that crossbred animals created to compete in international markets, such as the Japanese market, will have poorer values for growth traits and the least amount of saleable meat than animals from international beef breeds.

Regarding adaptation to subtropical regions, the use of crossbreeding between Zebu breeds (*Bos taurus Indicus*, which are well adapted to subtropical and tropical regions) and breeds of European origin (*Bos taurus Taurus*, adapted to colder climates and featuring greater weight gain and meat quality potential) can become an important tool to increase meat production and to improve quality factors, while maintaining an optimal level of adaptation affecting traits in subtropical regions (Prado et al., 2008).

Animals derived from the cross *Bos taurus*×*Bos indicus* have been evaluated under temperate conditions, where cows have adequate production performance (Cundiff et al., 1986). However, it also has been observed that these crossbred animals have less than desired performance for carcass composition and meat quality traits than *Bos taurus* purebred beef animals (Wheeler et al., 2001). Barros et al. (2003) evaluated the carcass characteristics and chemical composition of the LD muscle of *Bos indicus* and *Bos indicus* × *Bos taurus* crossbred steers. *Bos indicus* steers presented higher carcass yield and fat thickness compared to crossbreds. There was no breed effect on chemical composition of meat. Prado et al. (2008) evaluated the final weight, carcass characteristics, chemical composition and fatty acid profile in LD of young bulls of the crossbred type: Canchim×Aberdeen Angus, Nellore×Aberdeen Angus and Nellore×Continental breeds (Simmental, Limousin). Canchim×Aberdeen Angus and Nellore×Aberdeen Angus bulls had similar final body and hot carcass weights, while these were lower for the Nellore×Continental breed crosses. Fat thickness and LD area were inferior in the Nellore×Continental breed group. In contrast, lipid contents were higher in the LD of the Canchim×Aberdeen Angus bulls. Nellore×Aberdeen Angus and Nellore×Continental breed crosses featured a similar percentage of polyunsaturated, n-6 and n-3 fatty acids, and a larger ratio of polyunsaturated and saturated and n-6 and n-3 fatty acids in comparison to Canchim×Aberdeen Angus bulls. They concluded that the

use of British breeds (Angus) significantly increases fat deposition. Conversely, the use of Zebu breeds (Nellore) increases the percentages of polyunsaturated fatty acids, n-6 and n-3 fatty acids. Furthermore, the use of Zebu breeds improves the ratios of polyunsaturated to saturated fatty acids and of n-6 to n-3 ratio of fatty acids.

In the case of Spain, the Protected Geographical Indication (PGI) is traditionally based on rustic breeds. PGI is a regulation that promotes and protects names of quality agricultural products and foodstuffs; however, to improve growth, and principally carcass characteristics, Spanish breeds are often crossed to meat-improved breeds. In fact, although the PGI only presently admits purebred animals, the possibility of including crossbreds with meat-specialized breeds such as Charolais or Limousin is being considered. There are studies that compare carcass traits between Morucha and Morucha×Charolais (Vieira et al., 2006), Avileña and Avileña×Charolais (Panea et al., 2011); Retinta, Retinta×Charolais and Retinta×Limousin (García et al., 1995).

1.3.2 Dairy cattle.

Dairy production systems in most developed countries have almost exclusively consisted of purebreeding with a single breed, Holstein (Hansen, 2006). This domination was caused by its high production and good conformation traits (McAllister, 2002; Hansen, 2006) and over the last few decades, the North American Holstein has largely substituted the local strains cattle in Europe and in several other countries (Simm, 2000; Hansen, 2006).

Today the interest in crossbreeding increases due to changes in the dairy market towards broader breeding goals including functional traits and milk components, along with an increased level of inbreeding among purebred Holstein (Heins, 2007; Cassell and McAllister, 2009).

Some dairy producers are trying to improve functional traits and production traits through crossbreeding between Holstein with high milk production, and breeds with good fertility and health such as the Scandinavian Red, Normande or Montbeliarde, and thereby increase the profitability of the dairy production (Hansen, 2006).

In many dairy industries, selling calves for beef production has traditionally been seen as an important by-product (Simm, 2000) and therefore dairy cows are in some countries systematically inseminated with semen from beef cattle breeds to obtain a higher price for carcasses (Sørensen et al., 2008). The advantage of using beef × dairy crossbred for beef production is that it allows for faster growth of calves.

The higher growth capacity of the dairy×beef breed crosses compared to the purebred dairy breeds has been demonstrated in numerous studies (Andersen et al. 1977, More O'Ferrall and Keane 1990). For example, Huuskonen et al. (2013) estimated average daily gains improved in 7, 16, 20, 10, 13 and 17% with Holstein×Angus, Holstein×Blonde d´Aquitaine, Holstein×Charolais, Holstein×Hereford, Holstein×Limousin and Holstein×Simmental crossbreds, respectively, compared to purebred Holstein calves. Previously, Gerhardy et al. (1995) found purebred Holstein calves having 9% lighter at the age of 18 moths and had lower ADG than Charolais×Holstein crossbred calves.

With regard to carcasses characteristic, Huuskonen et al. (2013), found that Holstein×Angus and Holstein×Hereford crossbreds produced 41% and Holstein×Simmental crossbreds 54% better for carcass conformation than Holstein purebreds. With respect to other continental European breeds, the superiority of the Holstein×Limousin and Holstein×Blonde d´Aquitaine crossbred calves for carcass conformation compared to Holstein purebreds was reported by Keane et al. (1989).

Furthermore, Keane and More O'Ferrall (1992) observed that Holstein×Hereford and Holstein×Simmental steers conformed 36 and 40% better than purebred Holsteins, respectively. The carcass fat score was 25, 4, 33, 4 and 13% higher for Holstein×Angus, Holstein×Charolais, Holstein×Hereford, Holstein×Limousin and Holstein×Simmental crossbreds, respectively, compared to purebred Holstein.

Güngör et al. (2003) reported a higher dressing percentage in Piemontese x Holstein and Limousin x Holstein crossbreds than in purebred dairy cattle. In general, it was observed that carcasses of crossbreed are more valuable than carcasses of purebred dairy cattle (Wolfová, 2007).

In Japan, a country with surplus milk production, Holstein cows with low production are crossed with the Japanese Black beef breed to produce animals with a better carcass quality than purebred Holsteins (Kahi and Hirooka, 2006).

With regards to meat quality traits, Gerhardy et al. (1995) reported brighter L* in the *longissimus dorsi* (LD) values in Charolais×Holstein crossbred calves compared with Holstein calves. The observed animals in this study showed no differences in tenderness of the LD after 24 h. and reported similar shear force values in Charolais×Holstein and in purebred Holstein calves. No differences were recorded in the pH of the LD after 24 h between the investigated calves. Charolais crosses had a lower proportion of muscle lipids than the dairy strains studied, but there were no differences amongst the genotypes in sensory traits. Keane et al. (2001) indicated that there are few differences in meat quality amongst purebred dairy and beef×dairy cattle, but Davies et al. (1992) reported improved eating characteristics of meat, compared to the purebred dairy animals, when using crosses of a dairy breed with specialized beef breeds.

1.3.3 Sheep.

In sheep, as in the majority of farm animals, specialized maternal breeds emphasizes adaptability and reproductive traits and tends to be less extreme for carcass traits and mature weight. Breeds considered as specialized maternal breeds include Merino, Polypay, Rambouillet, and Targhee. Adaptability, longevity, mothering ability, and moderate mature weight are common characteristics of these four specialized maternal breeds. In addition, Finnsheep and Romanov are used exclusively as specialized maternal breeds primarily due to young age at puberty and very high lambing rates (about 3.0 and 3.7 lambs per ewe lambing for mature Finnsheep and Romanov ewes, respectively).

Rams of specialized paternal breeds are mated to purebred or crossbred ewes of specialized maternal breeds to produce market lambs in terminal crossbreeding systems. Specialized paternal breeds produce crossbred lambs that have desirable carcasses and growth rates that are optimal for specific production-marketing situations. Dorset Down, Hampshire, Ile-de-France, Merino Precoce, Oldenburg, Oxford, Shropshire, Southdown, Suffolk and Texel rams are commonly used as terminal breeds.

Kirschten et al. (2013) quantified differences in feed efficiency among Columbia, USMARC-Composite (Composite), Suffolk, and Texel rams mated with Rambouillet ewes. At 90 d, Suffolk-sired lambs had gained 13 to 19% more body weight, were 7 to 13% heavier, and had consumed 4 to 11% more feed than the other breed crosses. However, body weight gain was greater for Suffolk-sired lambs than for the other 3 sire breeds. Also, Columbia-sired lambs had the greatest residual feed intake.

With the same paternal breeds, Mousel et al. (2012) reported that Suffolk-sired lambs had heavier hot carcass, chilled carcass, and kidney weights than lambs sired by the

other breeds. Suffolk-sired lambs had more kidney-pelvic fat than Columbia-sired lambs; Composite- and Texel-sired lambs were intermediate and did not differ from the other crossbred lamb types. Texel- and Suffolk-sired lambs had larger LD area and better conformation scores than Columbia-sired lambs. Texel-sired lambs had greater body wall thickness, quality grades, and leg scores than Columbia-sired lambs. Composite and Suffolk-sired lambs did not differ from each other or from lambs sired by any other breed for body wall thickness, and were intermediate for quality grades and leg scores. Sire breed did not affect shipping shrink, dressing percentage, pelt weight, liver weight, or fat depth.

The effect of crossbreeding on lamb meat quality was examined by Hoffman et al. (2003) on LD and *semimembranosus* muscles of different lamb breed combinations. Dorper and Suffolk rams mated to Merino, Dohne Merino and Mutton Merino ewes gave six breed combinations. Ratings of sensory attributes on the *semimembranosus* muscle of the different lamb breed combinations were obtained from a trained descriptive panel. The moisture, total lipids, protein, ash, mineral content and fatty acid composition of the *semimembranosus* were also recorded. Physical parameters measured on the LD were: pH after 48h., drip loss, cooking loss and Warner-Bratzler shear force. Breed combinations did not have a significant effect on sensory quality of lamb, except the Dorper×Mutton Merino which showed a significantly higher initial juiciness than the Suffolk×Merino. Sire breed had a significant effect on pH after 48 h., Warner-Bratzler shear force, protein content and the fatty acid and mineral composition. With regards to protein content, the Dorper×Mutton Merino cross had the highest protein content. Dormer×Merino and Dorper×Dohne Merino had the highest and the lowest total SFA content, respectively. The researchers did not observe any significant difference for n-6 and n-3 PUFA across lamb breed combinations.

Producers could use these results to choose terminal sire sheep breeds that will complement their production system and improve market lamb value.

1.3.4 Goats.

Goat breeders commonly mate locally adapted does of the fecund-type maternal breeds (expressing a high frequency of multiple births) to sires of a meat-type. In practice, one-third of the does in the parental breed produces purebred offspring for herd replacements, while the remaining does are bred to sires of an alternate breed to produce crossbred kids for market. In this approach, the female parent, likely from an established breed in the region or indigenous population, can be raised within the farm, while the male parent with potential for increasing growth may be purchased from reputable breeders (Shrestha and Fahmy, 2007). Thus, some studies show the benefits of this specific breed crosses as Acharya (1988) in India, Zhou et al. (2001) in China, Abdelsalam et al. (1994) in Egypt, Gibb et al. (1993) in UK, Johnson et al. (1995) in USA or, Goonewardene et al. (1998) in Canada.

Crossbreeding of dairy breeds, such as the Alpine, Saanen and Toggenburg, with the Boer breed has considerable merit for use in goat meat production. Gibb et al. (1993), Waldron et al. (1995), Dhanda et al. (1999), Oman et al. (2000) and Shrestha and Fahmy (2007) recommended that kids not required as replacements be produced by using Boer sires to mate with purebred, crossbred or indigenous does. This would encourage dairy goat producers to improve growth traits and produce heavier carcasses for slaughter.

1.3.5 Pigs.

As for most prolific species, intensive pig production is based on a three-way production scheme. The most common cross is the one which uses F1 Landrace×Large White sows crossed with a terminal sire breed which provides either an outstanding carcass conformation or certain meat quality characteristics. Breeds like Pietrain or Belgian Landrace, are commonly used as terminal sires because they transmit genes for good conformation to the carcass, also Duroc boars are used because of their good meat quality (Blasco et al., 1994).

Many studies have measured growth, carcass and meat quality traits in crossbreeding schemes with terminal sire breeds. Blasco et al. (1994) studied five crosses: Landrace×Large White females crossed with Duroc, Large White and Belgian Landrace terminal sires, and Duroc×Large White females crossed with either Large White or Belgian Landrace sires. The cross with Duroc terminal sires grew faster and showed a better food conversion ratio. There were no significant differences in killing-out percent and carcass length. The Belgian Landrace progeny had the highest carcass lean content, the best carcass conformation and the highest proportion of ham and loin. Latorre et al. (2003) showed that Danish Duroc, as a terminal sire, grew faster and had better food conversion ratio than the other sires used (Dutch Duroc×Large White and Pietrain×Large White). Edwards et al. (2006) observed that Duroc-sired progeny were heavier compared to Pietrain-sired progeny, but had similar loin muscle area. Mean feed efficiency did not differ between breeds of sire. Duroc progeny had better average daily gains of age than Pietrain-sired pigs. Duroc-sired barrows tended to grow faster but with more fat tissue, and Pietrain-sired gilts were slower growing but were leaner, whereas Duroc-sired gilts and Pietrain-sired barrows were intermediate for growth and backfat

measures. Oliver et al. (2004) did not obtain differences in meat quality traits related to PSE conditions between Duroc and Large White terminal sires, but Belgian Landrace showed poorer meat quality and intramuscular fat content was higher in Duroc-sired pigs.

Some native porcine breeds from China, such as the Meishan, exhibit exceptional reproductive ability compared to currently used maternal genotypes and could be of great value for improving sow productivity (Legault and Caritez, 1983). However, these Chinese breeds are also characterized by very poor growth and carcass performance (Legault et al., 1985). Bidanel et al. (1993) confirmed the important disadvantage of crossbred Meishan pigs with respect to currently used genetic types for growth and carcass traits.

A special case involving meat quality traits involves the Iberian breed of pig (IB). Cured products from IB pigs are characterized by their high quality, but productivity of the sows is very low (less than 14 piglets weaned/sow/year) and also the fattening pigs are very inefficient (a feed conversion ratio higher than 5.6 for the fattening between 25 and 160 kg) (Serrano et al., 2008). Newton and Gill (1981) and Serrano et al. (2008) showed than Duroc-sired pigs grew faster and had better feed conversion than purebred IB pigs. Also, observed is that crossbreds from Duroc sires had more loin and more trimmed primal cut yields than purebred IB pigs. In the study by Serrano et al. (2008), IB pigs had lower ham weight losses during salting, postsalting, drying and ripening than Duroc crossbreds; this could be due to their higher fat content. Also, meat from purebred IB pigs was redder (a*) and lighter (L*) and had a more intensive colour (higher c*) than meat from Duroc-sired pigs. López-Bote (1998) reported that loins from Duroc crossbred pigs had more crude protein and less intramuscular fat than loins

from purebred IB pigs, but the fatty acids profile did not show differences between these genotypes.

1.3.6 Poultry.

Poultry broiler multinational companies usually provide to the farms chickens from a cross between White Cornish males and purebred White Rock females, or crossbred females coming from a cross between two strains of White Rock (Orozco, 1991). Recently, studies on broiler growth and feed conversion ratio were made to assess the usefulness of crossbred chickens between commercial and local strains in developing or tropical countries because broiler growth rate was severely depressed at high ambient temperatures (Deeb and Cahaner, 1996). Thus, the current breeding strategy for quality chickens in these countries uses crossbreeding between native breeds and highly-selected lines for rapid growth rate or relatively high egg production. The breeding objective focus has been on improving growth rate and reproductive efficiency while maintaining original appearance characters of native chicken such as plumage colour, body shape, comb shape, skin and shank colour to take into account consumer demand (Yang and Jiang, 2005). Numerous studies reported in developing countries have been on crossbreeding between exotic and native breeds (Kingori et al. (2010) in Kenya, Bekele et al. (2010) in Bangladesh, Saady et al. (2008) in Egypt, Mekki et al. (2005) in Sudan and Tadelle et al. (2000) in Ethiopia). However, breeding programs for local chicken breeds are difficult to set-up because of the competition with commercial breeding companies, which often have access to expensive technology and also the benefit of economics of scale (Saady et al., 2008). Islam and Nishibori (2010) reviewedthis issue and concluded that crossbreds involving locally adapted breeds may be useful for poultry production under semi-intensive systems in tropical climates

because of their adaptability, resistance to disease, better growth and meat yield traits compared to the exotic breeds or lines of chickens.

Recently, some studies have predicted the heterosis in a cross using high-density single nucleotide polymorphism (SNP) maps. Thus, Amuzu-Aweh et al. (2013) predicted heterosis in egg production traits in White Leghorn using SNP´s markers. The accuracy of the prediction for the heterosis of egg number and weight was ~0.5 that was considered acceptable, allowing the preselection of pure lines before field-testing, saving ~50% of field-testing cost with only 4% loss in heterosis. However, for the trait survival days, the accuracy was very low, and the method was discarded to predict heterosis for this trait.

1.3.7 Rabbits.

Efficiency of meat production can be improved by taking advantage of the diversity of rabbit breeds and lines through crossbreeding. There are studies whose objectives were to compare specific breed types, purebred and crossbred, for post-weaning growth, feed efficiency and survival traits.

In U.S.A., some studies evaluated the crossing between New Zealand White (NZW) and Californian (CA) breeds for post-weaning growth, feed utilization, and carcass and lean yield traits. Ozimba and Lukefahr (1991) evaluated NZW, CA, CAxNZW, Flemish Giant (FG)×CA and FG×Champagne D´Argent breed-types. They observed that purebred NZW litters consumed less feed than CA×NZW and FG crosses, gained less weight than FG crosses, and weighed less at 70 days as market fryers than CA×NZW and FG crosses. Feed intake was lower and average market weight was lighter for CA purebred litters than for CA×NZW and FG crossbred litters. The CA×NZW and FG crossbreds only differed for average market weight favoring the latter breed-type.

Roberts and Lukefahr (1992) evaluated CA, Champagne d'Argent, NZW and Palomino (PAL) as potential paternal breeds. They reported that PAL×NZW crossbred litters gained more slowly from 28 to 70 days than did CA×NZW crossbred litters. No differences were observed in the proportion of marketable fryers by 70 days among CA x NZW and PAL x NZW crossbred fryers.

Medellin and Lukefahr (2001) compared Altex and NZW and their reciprocal crossbreds for growth traits and reported that progeny of Altex sires were heavier at both weaning and 70 days and grew faster than progeny of NZW sires. Crossbreeding parameters (individual breed, maternal breed, and individual heterosis effects) were estimated. Altex sires increased weaning weight, average daily gains and slaughter weight by 40 g, 2.5 g/d, and 152 g, respectively. However, individual growth traits were not significantly influenced by maternal effects. Individual heterosis increased average daily gain (1.7 g/d) and slaughter weight (66 g).

In a Canadian experiment, Ouyed et al. (2011) compared different crosses among three rabbit breeds (NZW, CA and Chinchilla (CH)) for growth and carcass traits. Rabbits from NZW females mated to CA, NZW and CH males or from CA×NZW and NZW×CH crossbred females mated to NZW males ranked first for weight at weaning. Conversely, CH×CH and CA×CA purebred rabbits had the lightest weight at weaning. Rabbits from NZW females mated to NZW or CA males and from NZW×CH or CA×NZW females mated to NZW males had the heaviest slaughter weight. Rabbits with the poorest performance for slaughter weight and average daily gains were those coming from CA and CH females mated to CH males. Genetic types also affected feed consumption and feed efficiency. Rabbits from NZW×NZW, NZW×(CA×NZW) and NZW×(NZW×CH) genetic types showed the best feed conversion ratio. CH×CH rabbits had the lowest average daily feed consumption, but their slow average daily gains did

not allow for a good feed conversion ratio. Rabbits from CH×CA and CA×CA genetic types were those with the highest average daily feed consumption and best feed conversion ratio. Significant differences between genetic types were observed for all carcass traits except for meat/bone ratio. Rabbits from CH, NZW, CA×NZW and NZW×CH does mated to NZW males, and from NZW does mated to CA males had the heaviest cold carcass weight, which was higher by 20% than CH×CH rabbits, the less impressive breed for this trait. CH breed had unfavourable individual effects but favourable maternal effects on growth traits. CA breed had negative maternal effects on weight traits from weaning to slaughtering. Both CA and CH breeds had positive direct and negative maternal effects on yield of the carcass intermediate part compared to NZW. Positive individual heterotic effects were found for body weight traits, particularly in those crosses involving NZW breed, with a magnitude ranging from 5 to 10% of the parental mean.

There are also European studies on crossbreeding that involved lines of the Department of Animal Science (UPV, Valencia), and the lines of the Rabbit Science Unit (IRTA, Barcelona). A crossbreeding experiment among 5 selected lines (A, V, and Prat as maternal lines, and R and Caldes lines as paternal lines providing the terminal sires) was carried out to improve knowledge about the genetic determination of growth traits during the fattening period. Orengo et al. (2009), showed, on average, that genetic groups from lines selected for growth rate were heavier, had faster growth rate, had higher feed intake and better feed conversion ratio than the genetic groups that originated from crosses among lines selected for litter size. Crossbreeding parameters were estimated and maternal and individual heterotic effects were null or very low. Individual effects mainly regulated the expression of growth traits. Previously, Piles et al. (2004b) measured crossbreeding parameters for growth, feed efficiency and carcass

yield in an experiment between the Caldes and R lines. Kits of genetic type Caldes were lighter at 60 days of age, grew slower and ingested less feed than kits of genetic type R, Caldes×R and R×Caldes. Slaughter and cold carcass weights followed the same pattern: animals belonging to Caldes group were lighter than animals from Caldes×R and R groups, values being intermediate for the R×Caldes group. A significant difference was also found in dressing percentage between the genetic types Caldes×R and R, the lowest value corresponding to R animals, and with genetic types Caldes and R×Caldes were intermediate. The difference between individual effects was only significant for live weight at 60 days and daily feed intake. Neither heterosis nor maternal effects were significant for any of the traits analyzed.

Brun and Ouhayoun (1989) and Brun et al. (1994) evaluated 1077, 9077 and 1066 lines for growth and carcass traits in France (INRA, SAGA, Toulouse). The lines 1007 and 1066 were both selected for litter size, and the 9077 line was used as a control line for 1077. In contrast to line 1066, line 9077 had favourable individual effects on growth rate and slaughter weigh but unfavorable ones on carcass quality. The 1077 line exerted unfavourable maternal effects on growth rate, carcass weight and decreased carcass fatness through direct effects. Significant heterosis was found on weaning weight in all crosses (5%), on slaughter yield (2%) in 1077×9077 and 9077×1066 crosses and on growth rate (7%) in the cross between strains 1066 and 1077. Nofal et al. (1995), in Hungary, compared NZW, CA and their reciprocal crosses for carcass traits. Estimates of heterosis in dressing percentage, fore-quarters, loin region, hind-quarters, head, liver, giblets and abdominal fat were -0.2, -4.0, 3.5, 1.2, 0.1, -6.0, -0.8, and -14.4%, respectively.

Metzger et al. (2006) performed a crossbreeding experiment involving Pannon White and Hyplus as terminal sires for carcass traits. The body weight of the offspring of

Hyplus sires was heavier than that of the offspring of Pannon White sires. However, regarding the most important carcass traits, differences were in favor of rabbits originated from Pannon White sires; thus, the ratio of the LD weight to the reference carcass weight and the fat deposits were higher in rabbits derived from Pannon White sires.

Studies between the Department of Animal Science (UPV, Valencia) and research institutions from Egypt and Saudi-Arabia have also been carried out. In Egypt, V line was crossed to local lines. Abou Khadiga (2008) and Youssef et al. (2008) evaluated post-weaning growth traits in crossbreeding experiments involving line V, and Baladi Black or Baladi Red, respectively. Youssef et al. (2008) observed significant differences in individual effects between the two lines in favor of V line for body weight and daily gain during most age intervals between 4 and 12 weeks. All estimates of individual heterosis were positive and ranged from 4.9 to 16.7% for body weight and 14.4 to 29.5% for daily gains, but the estimates for maternal heterosis were, in most cases, significantly negative and ranging from 4.5 to 15.2% for body weight and from 20.6 to 36.9% for daily gains. Also, Afifi et al. (1994) studied post-weaning growth and carcass performance in a cross between NZW and Baladi Red. Heterosis estimates for most growth traits were significant and ranged from a 2.5 to 5.0% for body weight and from 0.7 to 9.5% for daily gains. No significant individual heretosis was observed for most carcass traits.

In Saudi Arabia a crossbreeding project involving the line V and the Saudi Gabali breed was carried out. Al-Saef et al. (2009) observed that estimates of individual effects were significant and in favor of V line rabbits for the majority of the traits studied, ranging from 3.8 to 9.0% for slaughter and edible carcass components, 3.4 to 10% for non-edible traits, -3.1 to 9.8% for tissues compositions, and -14.9 to 2.5% for meat

quality traits. Maternal effects were significantly higher for the V line. Grand-maternal effects were not significant for most traits studied. Heterosis estimates for non-edible traits were mostly positive but only significant for head weight (individual and grand-maternal heterosis), fur weight (grand-maternal heterosis), lung weight (maternal and grand-maternal heterosis) and visceral weight (maternal and grand-maternal heterosis). Estimates of individual, maternal and grand-maternal heterosis for meat weight were found to be consistent and positive (3.9, 4.5 and 5%, respectively), being associated with significant individual heterosis for fat weight (12.2%), maternal heterosis for meat bone ratio (4.5%), and maternal and grand-maternal heterosis for dry matter in meat. The estimates of individual heterosis for protein content in meat were significantly positive (1.4%), but the estimates for grand-maternal heterosis were significantly negative (-2.1%). For fat content in meat, the estimates of individual (-8.3%) and maternal heterosis (-11.9%) were significant, while for ash content, the estimates for maternal (23.7%) and grand-maternal heterosis (30.1%) were significant and positive.

Currently, there are maternal lines exhibiting competitive performance advantages in reproduction. These lines vary based on the history of their selection programmes. The procedures and criteria used for their foundation are also different, and the length of their selection different as well. To my knowledge, an experiment of crossbreeding using a large set of those lines in three-way crossing schemes and recording growth, carcass and meat traits of the progeny has not been investigated to date. The interest of such an experiment would be the estimation of the crossbreeding parameters in the practical context of the three-way cross, analysing the influences of the of the maternal lines, and recommending specific crossbreeding programs bases on parameter estimates.

1.4 GENETIC IMPROVEMENT IN RABBITS – SELECTION AND CROSSBREEDING

In rabbit production, as in pig or poultry production, the scheme for genetic improvement and its diffusion is pyramidal (Figure 4).

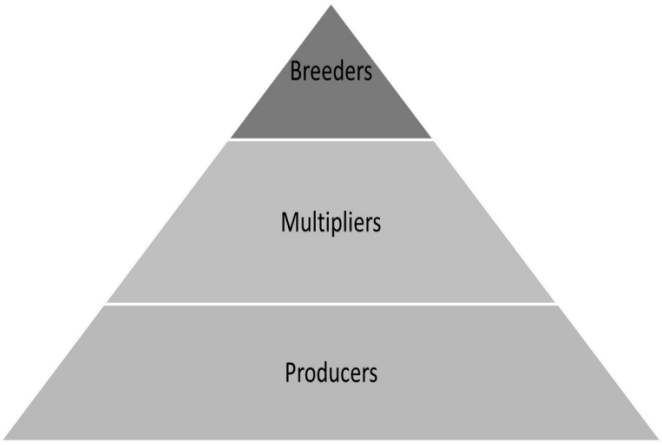

Figure 4. Rabbit industry breeding scheme

In the peak of the pyramid, called the nucleus of selection, is situated the specialized lines that are the base for obtaining the superior animals for production. The step immediately below corresponds to multiplication. This step serves as a link between the nucleus and the production farms. Unlike pigs, the multiplication companies in rabbits are not very common, being farmers who more often produce the does for production (Baselga and Blasco, 1989). Thus, these farmers have the advantage of reducing the costs of animals and diminishing the health and adaptation problems (Gómez et al., 1998).

In general, rabbit lines used for genetic improvement can be considered as maternal or paternal lines, which are used for meat production, following a three-way crossbreeding scheme. The first cross is between two maternal lines for the production of the crossbred female, which is used as doe stock for production on commercial

farms. The crossbred does are mated or inseminated to bucks of a paternal line to obtain the rabbits for fattening (Baselga, 2004).

Selection for rapid growth rate has been largely introduced to develop paternal lines to modify the whole pattern of growth, feed efficiency, and tissue composition, thus affecting carcass and meat quality traits (Khalil and Al-Saef, 2008).

Selection in paternal lines is done or should be done to improve the feed conversion ratio (FCR) because it is a critically economically important trait in meat rabbit production (Armero and Blasco, 1992; Cartuche et al., 2013). However in practice, post-weaning growth is an effective criterion of selection because it is very easy to record and it has a negative and favourable genetic correlation with feed conversion ratio (Piles et al., 2004a). The average daily gain is the preferred trait for selection during the post-weaning period, because this trait is less affected by common litter effects than individual weights at specific ages (Khalil and Al-Saef, 2008), which is also moderately correlated with FCR. Moura et al. (1997) stated that selection based on an index including both growth rate and feed conversion ratio would be more efficient for improving feed efficiency than selecting solely for growth rate. Other selection criteria considered recently in genetic improvement programs in paternal lines are the selection for residual feed consumption (Larzul and Rochambeau, 2005) and post-weaning growth under food restriction (Garreau et al., 2008). Selection for growth traits has made the growing period shortened, and the degree of maturity of rabbits is lower at slaughter weight (Pascual, 2007), whichpossibly can have a negative effect on carcass and meat quality indicators. In this light, other selection criteria related to carcass quality have been proposed. For example, Milisits and Levai (2002) applied the technique of TOBEC (Total Body Electrical Conductivity) to improve carcass

composition. A technique of X-ray computerized tomography was utilized to assess in vivo body composition

The selection criteria usually considered in selection programs of maternal lines are commonly related with reproductive traits, such as the number weaned or number born alive (Rochambeau et al., 1988; Estany et al., 1989; Gómez et al., 1996; Capra et al., 2000; El-Raffa, 2000; Baselga and García, 2002). In some cases, selection criteria included litter size at birth and weight at nine weeks (Bolet and Saleil, 2002) in order to counterbalance the negative effect of large litter sizes on individual weights. The number of teats (Rochambeau et al., 1988) has been considered as another selection criteria. Attention has been also posed on traits directly related with the ability of the doe for lactating and nourishing of the progeny, such as weight at weaning (Garreau and Rochambeau, 2003), litter weight at weaning or total milk production (Al-Saef et al., 2008; Iraqi et al., 2008; Youssef et al., 2008). Also, selection for ovulation rate and uterine capacity has been successfully performed as indirect ways for improving prenatal survival and litter size in rabbits (Ibañez et al., 2004, 2006; Blasco et al., 2005; Mocé et al., 2005; Santacreu et al., 2005).

The selection methods in maternal lines are more complicated than for paternal lines because males do not affect litter size traits, and heritability of reproduction traits is so low that it is necessary to consider as many records as possible on the individual and on relatives during the genetic evaluation of the does and bucks (Baselga, 2004). Also, purebred performance in the nucleus is, in some cases, a poor predictor of future crossbred performance on commercial farms (Ibañez-Escriche et al., 2011) due to the existence of genotype by environment interaction. To overcome these limitations, Wei and van der Steen (1991) and Lo et al. (1993) proposed combining crossbred and purebred selection (CCPS), in which phenotypic data collected on crossbred relatives

are used for selection of purebreds. Thus, the application of a CCPS system, that until now has not been applied in rabbits, offers much potential as follows (Ibañez-Escriche and Noguera, 2013):

a) The selection response is proportional to the precision of the estimated breeding value (Falconer and Mackay, 1996). The adequate incorporation of crossbred animals can improve the precision of estimated breeding value, and therefore the selection response.
b) CCPS can reduce the generational interval (Wei and Van der Werf, 1994), whereupon the selection response per unit of time is higher.
c) Crossbred data permit for estimation of dominance effects and the combinatory aspects of candidates for selection. This information allows selection of candidates not only for their estimated breeding value, but also for their dominance or combinatory values.
d) CCPS enables the incorporation of important economic traits such as meat quality in genetic programs. Moreover, it is also important to note that these traits can be controlled in animals under commercial conditions, being different than the environmental conditions in the nucleus.

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CHAPTER 2. OBJETIVES

The aim of this thesis was to estimate differences and crossbreeding parameters for post-weaning traits of crossbred rabbits, the dams of which are derived from a full diallel-cross among four maternal lines (16 genetics groups) and the sires from a paternal line. This general objective was partitioned into the following specific objectives:

a) To compare the four maternal rabbit lines in terms of growth traits at foundation and at fixed times during their selection processes for reproductive traits.
b) To compare the 16 genetic groups and estimate crossbreeding parameters for body weight, post-weaning average daily gains, feed intake and feed conversion ratio in the fattening period of crossbred rabbits.
c) To compare the 16 genetic groups and estimate crossbreeding parameters for slaughter and carcass traits.
d) To compare the 16 genetic groups and estimate crossbreeding parameters for meat quality traits.

CHAPTER 3

Growth traits of four maternal lines of rabbits founded on different criteria. Comparisons at foundation and at fixed times after selection.

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3.1 ABSTRACT

The objective of this study was to compare growth traits (weaning and slaughter weights and average daily gain) in four Spanish maternal lines of rabbit (A, V, H and LP) founded under different criteria, but all of them selected for litter size at weaning. Cross-fostering was never practiced. These lines are, at present, in the 43th, 38th, 22th and 8th generations, respectively. A Bayesian approach was used for inference determination. Two comparisons were performed. One compared the values of the lines at their origins, using the complete data set (data from June 1980 to September 2012), the full pedigree and a two-trait analysis, with number at weaning, thus the selection process was accounted for. The other type of comparison was done during the last period when all the lines were housed and measured together at the nucleus location, having the same feeding and management environment (from March 1997 to August 1998 for the lines A, V and H and from December 2009 to September 2012 for the lines A, V and LP). The second analysis used only the data corresponding to each time period, which was conducted using one-trait models. These models were the same than the ones referred for the comparisons at the origin, but the additive effects were excluded. Estimates of the genetic correlations between litter size at weaning and growth traits were positive but low (0.29 for weaning weight, 0.13 for slaughter weight and 0.15 for average daily gain). The contrast between the lines showed that at the origin and in the fixed periods, the H and LP lines had the highest values of the traits.

These differences may be due to the different criteria and processes used to establish the lines. In the fixed periods, the observed (computed with the records of each period) and the expected differences (computed with the complete model and data set) were very similar for all traits, indicating the suitability of the used models. At each period, the differences between lines for growth traits were smaller than at the origin. This result could be a consequence of a correlated response on growth due to selection for litter size at weaning, as well as to direct response to a concomitant, non-programmed selection effect for growth traits, being different in intensity between the lines and (or) to genetic drift.

Keywords: line foundation, litter size, growth traits, maternal lines, rabbits.

3.2 INTRODUCTION

The organization of genetic improvement programmes for rabbits has a pyramid structure; the populations in the nucleus are specialized lines (maternal and paternal lines), selected for reproduction and growth traits, respectively. Meat production is based on a three-way crossbreeding scheme using for the cross the maternal and paternal lines selected at the nucleus level. The criteria of selection for maternal lines is usually based on litter size at birth or at weaning (Rochambeau et al., 1994; Garreau et al., 2004) and for the paternal lines post-weaning daily gain or some weight close to slaughter time (Rochambeau, 1988; Baselga, 2004). All these traits are of clear economic importance (Armero and Blasco, 1992; Cartuche et al., 2013). Although maternal lines are not usually selected for growth characteristics, it is important to take into account how these traits are affected by the foundation of the maternal lines and through their subsequent selection course for reproductive traits. Another consideration

is that crossbred does provide 50 % of their genes to rabbits for slaughter, therefore maternal lines should also show an acceptable level for growth traits. Comparisons between lines are feasible for periods of time at which the lines have the same housing and management environment. Some of these differences could be due to initial differences between the lines of origin as a consequence of their foundation history. In this sense, it could be useful to estimate these differences. This is possible when several lines share the same farm environment for long periods of time using all the data recorded since the foundation of the lines and the genetic models accounting for the effect of selection.

Thus, the objective of this study was to estimate differences in growth at determined periods of time in four maternal lines of rabbits selected for litter size at weaning, relating these differences to their unique foundation. In addition, the heritabilities of the growth traits and their genetic correlation with litter size at weaning will be estimated.

3.3 MATERIAL AND METHODS

3.3.1 Animals

The present study involved four Spanish maternal lines of rabbits, housed on the farm of the Animal Science Department of the Polytechnic University of Valencia (Spain). These lines, after their foundation, have been selected to increase litter size at weaning. The analysis included all the data recorded from the 1st generation to the current, 43^{th}, 38^{th}, 22^{th} and 8^{th} generations for lines A, V, H, and LP, respectively.

The animals of A, V and LP lines have been maintained as closed nucleus populations from the beginning of the selection process for prolificacy up to the present and housed at the same Valencia farm as mentioned above. The H line was also

maintained as closed from foundation and was housed at the same farm until its 10th generation of selection (May 2004) when it was moved to another farm 180 km north of Valencia (San Carlos de la Rápita, Tarragona).

Line A 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 breeds of rabbits used for meat production. The criteria used to form line A were that the founders were healthy and they fulfilled the standards of the NZW breed. Since 1980, the line has been selected for prolificacy at weaning using a family index (Estany et al., 1989). Line V was established from four different synthetic maternal populations in 1984, crossing crossbred males of two types with crossbred females of two other types. Selection candidates were 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 evaluation procedure was used for LP and H lines. Line H was founded by applying hyperprolific selection and embryo cryopreservation techniques (Cifre et al., 1998a). The hyperprolific does, used in founding this line, were assembled from several large commercial populations. The LP line was founded by selecting females, no matter their genetic type, from commercial farms that showed an extremely long productive life (measured as a function of the number of parities) associated with prolificacy (measured as the mean number of young born alive per parity) near or above the average of the Spanish commercial rabbit population (Sánchez et al., 2008).

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

first mated around 17 weeks of age, females were serviced 10 - 12 days post-kindling and a pregnancy test was carried out by abdominal palpation on day 12 after mating. There was an exception to this mating management for lines V and LP from December 2003 to November 2005 when does were mated 25 days after kindling. Thus, the minimum parturition interval that could be achieved was around 40-42 days. Does which did not accept the buck were presented to the male one week later and does that were not diagnosed as pregnant after abdominal palpation, were also returned to the male for a repeat mating. Does which did not get pregnant after two such matings were culled. Mates were not allowed to have common grandparents. The animals from these four lines are extensively used as maternal grandparents (lines A, V, H and LP) in the 3-way cross scheme for commercial meat rabbit production in Spain.

The equipment used in the nucleus farm was the same for all lines, except that the feeders used from September 1998 to November 2003 were different for the H line. These feeders were designed to minimize the feed spillage but the access to the feed was more difficult.

Litters were reared by their dams, without fostering, for about 28 days. At weaning, rabbits were individually identified by a number tattooed on the ear and placed in collective cages (80cm long, 50 cm wide, 30cm high) of about nine rabbits until marketing at 63 days. During post-weaning period, rabbits were fed *ad libitum*, with a standard commercial pelleted diet and fresh water.

3.3.2 Data recording and statistical model

The growth traits studied were weaning weight (**WW,** g at 28 d), slaughter weight (**SW**, g at 63 d) and average daily gain between weaning and 63 d (**ADG**, g/d). The number of records were 323,208 for WW, and 300,553 for SW and ADG. These records

were from 46,708 litters, for which number of born and weaned rabbits were also recorded. The pedigree file included 346,638 animals (108,386; 164,483; 36,251 and 37,518 for A, V, H and LP, respectively). In the pedigree, the number of sires was 1149, 1136, 416 and 266 for A, V, H and LP lines, respectively, and the corresponding number of dams was 4741, 5320, 1448 and 952, respectively.

To avoid selection bias during the estimation of both variance components and contrasts between lines (Sorensen and Johansson, 1992), the analyses of WW, WS and ADG were carried out jointly with litter size at weaning, the selection criteria in all the lines, using a two-trait model.

The model for growth traits was:

$$Y_{jklmn} = LYS_j + OP_k + b \times NV_n + a_l + m_m + lo_n + e_{jklmn} \quad \text{(Model 1)}$$

Where: Y_{jklmn} is the record of the trait of animal *l*; LYS_j is the effect of line-year-season combination, line of animal *l* and the year-season of parity (one year-season every 3 month: 298 levels for all lines); OP_k is the effect of the order of parity (5 levels: 1st, 2nd, 3rd, 4th, and >4th), NV_n is the number of born alive in the litter in which the young rabbit was born and b is the regression coefficient on this covariate; a_l is the random additive value of animal *l*; m_m is the environmental random effect of its dam (animal *m* is the dam to the individual *l*); lo_n is the random effect of the litter in which the animal was born and e_{jklmn} is the residual effect. A sex effect was not included because sexual dimorphism in rabbits is thought to either not exist or to arise only late in life (Ozimba and Lukefahr, 1991).

The model for litter size at weaning was:

$$NW_{jkl} = LYS_j + EF_k + a_l + p_l + e_{jkl} \quad \text{(Model 2)}$$

Where: NW_{jkl} is the litter size at weaning of a parity of doe l, EF_k is the effect of the physiological state of the doe (5 levels: nulliparous, primiparous lactating, primiparous non-lactating, multiparous lactating and multiparous non-lactating), p_l is the random, permanent, non-additive genetic and environmental effects of the doe l. The other components of the model were defined above.

The correlation structure between the random effects in the two models was established between the additive effects of the two traits; between the non-additive genetic and environmental maternal effect of growth traits (m_m) and the permanent non-additive genetic and environmental effects of the doe on litter size at weaning (p_l). Also, to specify the environmental covariance structure between each of the growth traits and NW, the term e_{jkl} of NW model was divided into two parts, c_{jkl} and e^*_{jkl}, for the first it was assumed that these effects were correlated with the litter of origin effect in the growth trait model (lo_n) and the second were uncorrelated (García and Baselga, 2002b) to any other term of the model fitting the growth trait. A Bayesian analysis was performed.

The joint prior distribution assumed for additive genetic effects was $N(\mathbf{0}, \mathbf{G_a} \otimes \mathbf{A})$, where $\mathbf{G_a}$ was the genetic (co)variance matrix between the traits and $\mathbf{A}$ was the additive genetic relationship matrix. The prior distribution for the permanent non-additive genetic and environmental effects of NW (p_l) and the maternal effect of growth trait (m_m) was $N(\mathbf{0}, \mathbf{G_p} \otimes \mathbf{I})$, where $\mathbf{G_p}$ was the (co)variance matrix between

these effects. The joint prior distribution for the litter of origin effect (lo_n) in the growth trait and the term c_{jkl} was $N(\mathbf{0}, \mathbf{G}_{lo} \otimes \mathbf{I})$, where $\mathbf{G}_{lo}$ was the (co)variance matrix between these litter effects. The residual prior distribution was $N(\mathbf{0}, \mathbf{I}\sigma^2_{e*})$ for the NW model and $N(\mathbf{0}, \mathbf{I}\sigma^2_e)$ for the growth trait model, $\mathbf{I}$ is an identity matrix of order equal to the number of records measured in each case.

As well as for the systematic effect, uniform priors were considered for all the variance components. Statistics of the marginal posterior distributions of all unknowns were obtained using the Gibbs Sampling algorithm. The software used for Gibbs Sampling was gibbs2f90 (Misztal et al., 2002). After some exploratory analyses, chains of 250,000 samples were run and the first 25,000 iterations were discarded as the burn-in period in order to allow for the algorithm to reach convergence to the marginal posterior distributions. Afterwards, one sample in each 25 was saved to avoid high correlations between consecutive samples. Monte Carlo SE was computed for the chain of each parameter of interest. Details of the procedure can be found in Blasco (2001) and in Sorensen and Gianola (2002).

Marginal posterior distributions were characterized by computing the mean, the standard deviation, the highest posterior density region covering 95% of the density (**$HPD_{95\%}$**), and for the contrast between lines, whereas the probability of the difference between lines being greater than zero was also acquired.

3.3.3 Comparison of lines at their foundation

Similarly to Ragab and Baselga (2011), from the solutions for LYS effects, differences between each pair of lines at origin were calculated. In order to do this, the appropriate estimable function included the difference between the averages of the

levels of LYS in which the rabbits of the two lines involved in the comparison coexisted and shared the same environmental conditions. Because the model of analysis included the additive genetic effect, the differences between the lines directly refer to the time since their respective foundations. The periods in which the different lines coexisted and shared identical environmental conditions were: from June 1982 to September 2012 for A and V lines, excepting the period between December 2003 and November 2005; from June 1996 to June 2004, for lines A and H, except for the period between September 1998 and November 2003, and from December 2005 to September 2012 for lines A and LP. The common farm-year-seasons for lines V and H were between June 1996 and August 1998; and from December 2003 to September 2012 for the lines V and LP. Between H and LP lines, the contrast was not done because they only shared two years-season. Within the framework of a Bayesian MCMC analysis it is possible to get samples from the marginal posterior distributions of the contrast at the foundation by applying the appropriate contrast matrix to the solution vector sampled in each round of the Gibbs Sampler.

3.3.4 Comparison of lines at fixed times (observed and expected differences)

The chosen periods for the current comparison of the lines at fixed times were the last six farm-year-seasons in which at least three lines shared the same farm location and environmental conditions. This comparison was made in two periods: from March 1997 to August 1998 for lines A, V and H (Period 1), and from June 2011 to September 2012 for lines A, V and LP (Period 2). This comparison was made in two different ways. In the first, the additive genetic effects were excluded from the model, and only the data recorded during the considered periods were used. The estimable functions defined for obtaining the contrast were calculated in the same way as for the differences

at origin, and were called observed differences because its computation was independent of the genetic model and used only for the data period of comparison. In the second, the results obtained with the complete model and data set were used to do the line comparison, and the differences computed were called expected differences. This was done by adding to the difference between the averages of the levels of LYS shared by both lines in the period of comparison, the difference between the averages of the estimated breeding values of the animals of each line present in that period. The first part of this summation represents the differences at the foundation between the animals in the comparison, while the second term represents different correlated responses to the selection process. For both observed and expected differences it is possible within the framework of a Bayesian MCMC analysis obtain statistics of their marginal posterior distributions.

The comparison between expected and observed differences allows for the acquisition of evidence or validity regarding the appropriateness of the genetic models used for studying this data set; a high similarity between these two quantities would indicate satisfactory performance of the models used to predict breeding values.

3.4 RESULTS AND DISCUSSION

3.4.1 Descriptive statistics

Summary statistics for all traits are shown in Table 1 which take into account the entire data. There are two important results to be noted. One is the large number of data that were involved, covering extremely long selection periods. If only data from the current generation were retained then higher weaning prolificacy would have been observed. The averages of NW in generations 43^{th}, 38^{th}, 22^{th} and 8^{h} of the lines A, V, H

and LP were 8.4, 8.2, 8.8 and 8.3 kits, respectively. The increase with respect to the overall average is clear and it is partially a consequence of the success of the selection process. The other important result to be noted is that despite all the maternal lines having acceptable mean levels for growth traits, which are characters that were not directly selected for, the growth performance is clearly lower than that of paternal lines, and are also out of the range of commercial weights in Spain (e.g., SW mean is between 2 and 2.3 kg) (MAGRAMA, 2012). This can be explained because, on the one hand, the commercial production of rabbit meat usually relies on a crossbred schema that involve a paternal line selected by growth rate. Feki et al. (1996) compared the paternal line R, selected for postweaning daily gain from 28 to 63 d, after 19 generations of selection with lines A and V, which were selected for 18 and 14 generations for litter size at weaning, respectively. They observed superiority of the R line for WW and ADG by 74 g and 10.1 g/d, respectively. In addition, on commercial farms the slaughter day is defined by weight while in these nucleus populations slaughter weight was recorded at a fixed age of 63 days.

Table 1. Descriptive statistics for litter size at weaning (NW), weaning weight (WW, kg), slaughter weight (SW, kg) and average daily gain (ADG, g/d)

	N[2]	Mean	SD[3]	Minimum	Maximum	[4]ß/NW
NW[1]	46,708	7.84	2.95	0.00	16.00	
WW	323,208	0.57	0.13	0.10	1.30	-0.03(0.00)
SW	300,553	1.86	0.26	0.80	3.46	-0.02(0.00)
ADG	300,553	36.7	5.7	3.4	79.4	-0.20(0.05)

1. NW statistics refers to litters; [2]. N= number of rabbits; [3]. SD= standard deviation; [4] Regresion coefficient (S.D.)

The average age of the animals when reaching slaughter weight in commercial populations is slightly higher, around 66 days (MAGRAMA, 2012).

3.4.2 Variance components

Heritability estimates are shown in Table 2. These estimates (marginal posterior mean ± marginal posterior standard deviation) were 0.06 ± 0.00 for NW (average for the three analyses), 0.07 ± 0.00 for WW, 0.19 ± 0.00 for SW and 0.21 ± 0.00 for ADG. The small value of the marginal posterior standard deviations was noteworthy, this was obviously the result of the large number of records.

Table 2. Statistics of the estimated marginal posterior distributions of the heritability (h^2) for litter size at weaning and growth traits.

Trait	Mean	SD[1]	$HPD_{95\%}$[2]	MCE[3]
NW	0.061	0.005	0.051 , 0.069	0.001
WW	0.065	0.005	0.054 , 0.075	0.001
SW	0.191	0.009	0.174 , 0.209	0.001
ADG	0.206	0.008	0.190 , 0.221	0.001

NW= litter size at weaning; WW= weaning weight; SW= slaughter weight; ADG= average daily gain; [1]. SD = standard deviation; [2] . $HPD_{95\%}$ = highest posterior density region at 95% of probability; [3] . MCE = Monte Carlo error.

Rochambeau et al. (1994) for the A1077 and A2066 lines; Rastogi et al. (2000) for the New Zealand (NZW) breed; Sorensen et al. (2001) for the Danish White breed; Piles et al. (2006) for the A, V and Prat lines; Sánchez et al. (2006) for the LP line, and Ragab and Baselga (2011) for lines A, V, H and LP showed similar estimates of heritability for NW. Lower estimates were obtained by Baselga et al. (1992) for the A and V lines; Ferraz and Eler (1996) for NZW and Californian (CAL) breeds; Gómez et al. (1996) for Prat line; Moura et al. (2001) for the Botucato breed, and Youssef et al. (2008) for V and APRI lines. However, García and Baselga (2002b) found higher values for line A.

Estany et al. (1992), for the R line, obtained a higher heritability for WW, while for SW and GMD they found the same magnitude of heritability. For diverse lines, the

bibliography showed higher values of heritability for all the growth traits studied (Ponce de León and Gusmán, 1999, for CAL, Chinchilla and NZW breeds; Rochambeau, 1988, for A1077 and A2066 lines).

These differences in the estimates of heritability can be attributed to the different methods (models) of estimation, differences in variability of the lines at foundation, environmental effects or sampling errors due to the small sample size used in some studies. Also, our study involved 4 lines and these heritabilities could be interpreted as an average of the heritability of the lines. The estimates of the variance ratio involving the permanent non-additive genetic and environmental effects (p^2) for NW and the non-additive genetic and environmental maternal effects for growth traits (m^2) are shown in Table 3. The estimates for p^2 were low, and had the same magnitude as in García and Baselga (2002b), Sánchez et al. (2006), Al-Saef et al. (2008) and Ragab and Baselga (2011). The repeatability estimate (sum of h^2 and p^2) for NW was 0.15, which is in the rank of Rochambeau et al. (1994), García y Baselga (2002b), Al-Saef et al. (2008) and Ragab and Baselga (2011). The estimates for m^2 were also low and decreased between weaning and slaughter age (Cifre et al. 1999; Su et al. 1999).

Table 3: Statistics of the estimated marginal posterior distributions of the proportions of the permanent effect variance (p^2) for NW and the total maternal effects variance (m^2) for growth traits with respect to their phenotypic variances.

Trait	Mean	SD[a]	$HPD_{95\%}$[b]	MCE[c]
NW p^2	0.096	0.009	0.079 , 0.114	0.001
WW m^2	0.112	0.004	0.104 , 0.119	0.001
SW m^2	0.041	0.003	0.036 , 0.047	0.001
ADG m^2	0.003	0.001	0.002 , 0.004	0.001

NW= litter size at weaning; WW= weaning weight; SW= slaughter weight; ADG= average daily gain; [a]. SD = standard deviation; [b] . $HPD_{95\%}$ = highest posterior density region at 95% of probability; [c] . MCE = Monte Carlo error.

The estimates of the ratio between the common litter effect variance and the phenotypic variance (c^2) are shown in Table 4. The common litter effect includes aspects attributable to each pregnancy and birth of the female: uterine environment, milk production or maternal behaviour, but not the litter size in which each rabbit was born, because this effect was included as a covariate in the model. The estimates of c^2were lower than those reported by García and Baselga (2002b) for WW, but for SW and ADG they found estimates of similar magnitude to ours. The estimates for c^2 were higher than the heritability estimates because, in rabbits, a non-negligible part of phenotypic variation in growth and feed efficiency is a consequence of environmental effects related to the dam or the litter. These results agree with previous findings by McNitt and Lukefahr (1996), and García and Baselga (2002b). The importance of maternal and litter-specific effects for traits recorded in the fattening period is consequence of the short interval of time between weaning and slaughter.

The loss of relevance of common litter and maternal effects with respect to other effects, direct additive genetic effects, along the growth of the animal has been documented by other authors (Masoero, 1982; Camacho and Baselga, 1990; Ferraz et al, 1996; McNitt and Lukefahr, 1996). In our study this happened for both maternal and common litter effects, especially for the maternal effect; these two parameters drastically declined between WW to SW.

Table 4: Statistics of the estimated marginal posterior distributions of the proportions of the common litter effect variance (c^2) for growth traits with respect to their phenotypic variance.

Trait	Mean	SD[1]	$HPD_{95\%}$[2]	MCE[3]
WW	0.355	0.003	0.348 , 0.362	0.001
SW	0.256	0.003	0.250 , 0.261	0.001
ADG	0.286	0.003	0.279 , 0.291	0.001

WW= weaning weight; SW= slaughter weight; ADG= average daily gain; [1]. SD = standard deviation; [2] . $HPD_{95\%}$ = highest posterior density region at 95% of probability; [3] . MCE = Monte Carlo error.

Thus, in rabbits, the influence of maternal and litter effects is exerted prior to slaughter age on any body weight measurement; however, it has been reported that the influence of these effects on ADG is lower (Piles et al., 2004). ADG is computed as a difference between two weights and both share common litter and maternal effects, which basically accumulated from the lactation period, thus when computing the difference for obtaining ADG these effects are cancelled out. We have observed that this happened also for maternal effects while no maternal effects on ADG were obtained; however, this was not the case for common litter effects. This result could be expected if it is taken into account that the actual contact between a dam and its progeny end at weaning but the litter mates continue to share environmental conditions during the fattening period. For instance, in our case all or the majority of litter mates at weaning were located in the same cage.

Genetic, permanent and residual correlation estimates are shown in Table 5.

Table 5: Statistics of the estimated marginal posterior distributions of the genetic (r_g), permanent (r_p) and residuals effects (r_e), and correlations between growth traits and litter size at weaning (NW).

Trait	Parameter	Mean	SD[3]	$HPD_{95\%}$[4]	MCE[5]
WW	$\mathbf{r_g}$	0.299	0.071	0.139 , 0.412	0.009
WW	$\mathbf{r_p}$[1]	-0.335	0.035	-0.403 , -0.266	0.002
WW	$\mathbf{r_e}$[2]	-0.770	0.074	-0.908 , -0.667	0.009
SW	$\mathbf{r_g}$	0.132	0.057	0.014 , 0.233	0.006
SW	$\mathbf{r_p}$[1]	-0.147	0.055	-0.252 , -0.038	0.004
SW	$\mathbf{r_e}$[2]	-0.687	0.139	-0.973 , -0.520	0.012
ADG	$\mathbf{r_g}$	0.145	0.058	0.028 , 0.254	0.006
ADG	$\mathbf{r_p}$[1]	0.973	0.054	0.848 , 1.000	0.007
ADG	$\mathbf{r_e}$[2]	0.508	0.144	0.259 , 0.757	0.018

[1]Correlation between permanent effects for NW and maternal effects for growth traits; [2]Correlation between residual effects for NW and common litter effects for growth traits; WW= weaning weight; SW= slaughter weight; ADG= average daily gain; [3]. SD = standard deviation; [4] . $HPD_{95\%}$ = highest posterior density region at 95% of probability; [5] . MCE = Monte Carlo error.

The genetic correlations between NW and all growth traits were positive but low. These low or null genetic correlations between litter size and growth traits have also been observed by Matheron and Poujardieu (1984) and García and Baselga, (2002b). These results are also in agreement with García and Baselga (2002a) who showed that selection for litter size did not significantly change the phenotypic values of growth traits analyzed with constant litter size. Permanent and residual correlations between WW and NW, and between SW and NW, were negative and higher in absolute value than the corresponding genetic correlations. This would be expected if we accept that environmental factors that increase the NW tend to reduce WW and SW. Contrary to this, permanent and residual correlations between ADG and NW were positive and high, particularly those between permanent effects on NW and maternal effect of ADG,

which could likely be an expression of compensatory growth (Testik et al., 1999; Belhadi, 2004).

3.4.3 Contrasts between lines at foundation

Tables 6, 7 and 8 show the contrasts between the lines A, V, H, and LP for the different growth traits. These contrasts are estimable functions between pairs of lines over year-season classes in which both lines coexisted on the farm with the same equipment and were subjected to identical management conditions. The contrast between H and LP lines was not done because they only shared two year-seasons on the same farm. The estimates of the effects of line-year-season combination, needed for the contrasts, were obtained by an analysis that took into account all the data, including the permanent non-additive genetic and environmental effects (maternal and litter at origin) and the additive effects. As the additive effects of the animals were considered in the model, the selection response was accounted for by this effect, and consequently, the effects of the lines (included in the line-year-season combination) expressed the genetic values at their foundation.

The contrasts A-V showed that line A was superior to line V, with a probability of this contrast being greater than 0 of 0.99, 0.97 and 0.75 for WW, SW and ADG, respectively. Given these probabilities, HPD 95% for ADG and SW are expected to include zero, which actually happened. Feki et al. (1996) obtained higher values for weaning weight in favor of the A line with respect to the V line, but in this case the differences were not at foundation, and no correction for litter size was conducted in the statistical model.

For growth traits, the contrasts between the H and LP lines with lines A and V (A-H, V-H, A-LP and V-LP) reveal that the lines H and LP were the heaviest with a

probability of zero or near zero of these contrasts to be greater than 0. Only for WW in the contrast A-H, the zero was included in the HPD 95%. Cifre et al. (1998b) compared the H line at foundation with the contemporary generation of the V line and they found that the H line was always significantly heavier than the V line for WW, and had also a higher mean for SW, although the mean ADG was not significantly different. It must be noted that in this case the interaction line-year-season was not fitted into the model. Considering the procedures for founding A, V, H and LP lines these results make sense, the first two lines were created from NZW (line A) and from maternal lines (line V), while the last two were created apparently from crossbred does from meat rabbit commercial populations. These does should be true crossbreds of two maternal lines, but sometimes the farmers select replacements with does that are progeny of true crossbred does and bucks of a paternal line. The frequency of this event can be assumed to be non-negligible when the price of rabbit meat is low (Ramón and Rafel, 2002).

Table 6: Observed and expected differences between the effects of the line at foundation and at fixed times for weaning weight (WW g).

		FOUNDATION				March 1997 - August 1998				June 2011 - September 2012			
	Contrast	**Mean**[1]	**SD**[2]	**HPD$_{95\%}$**[3]	**P>0**[4]	**Mean**	**SD**	**HPD$_{95\%}$**	**P>0**	**Mean**	**SD**	**HPD$_{95\%}$**	**P>0**
	A-V	28	12	4 , 53	0.99	22	5	13 , 31	1.00	0	7	-12 , 14	0.54
	A-H	-24	14	-47 , 7	0.07	2	5	-9 , 11	0.60				
EXPECTED	**V-H**	-59	14	-88 , -30	0.00	-20	5	-30 , -10	0.00				
	A-LP	-66	16	-93 , -33	0.00					-44	6	-56 , -31	0.00
	V-LP	-120	16	-156 , -93	0.00					-45	6	-56 , -34	0.00
	A-V					17	5	7 , 26	1.00	-7	8	-21 , 8	0.17
	A-H					-4	5	-14 , 7	0.25				
OBSERVED	**V-H**					-20	5	-30 , -11	0.00				
	A-LP									-53	7	-68 , -39	0.00
	V-LP									-46	6	-58 , -34	0.00

[1]. Mean = Marginal Posterior Mean [2]. SD = Marginal Posterior Standard Deviation; [3]. HPD$_{95\%}$ = Marginal Posterior highest density region covering 95% of the density ; [4]. P>0 = probability of the difference being greater than zero.

3.4.4 Contrasts between lines at fixed times (observed and expected differences)

Tables 6, 7 and 8 also show the contrasts between A, V and H lines for the different growth traits for the most recent periods in which at least three lines were present on the same farm (March 1997 to August 1998 and from June 2011 to September 2012 for lines A, V and LP). For both periods, expected differences are also presented.

From March 1997 to August 1998 the contrasts involving H line (A-H and V-H) indicated that this line was the heaviest with a probability of 0 of the contrasts being positive, the only exception to this was the contrast A-H for WW that had a probability equal to 0.25 (its $HPD_{95\%}$ included 0) of being positive. Similarly, from June 2011 to September 2012, the contrasts involving LP line (A-LP and V-LP) showed that this line was the heaviest. The contrasts between A and V lines were done in both periods, in the 1997-1998 period, regarding WW, line A was clearly heavier than V line, the probability of this contrast being greater than 0 was 1. However, in the 2012 period, the heaviest line at weaning was V, with a probability of only 0.17 of this contrast being in favor of the A line. Line V showed better results than line A for SW and ADG in the two periods. Expected results match well the observed differences between lines in both periods of the current comparison. This indicates the suitability of the genetic model that was used for the prediction of breeding values and the estimation of the differences between the lines at origin. In this sense, assuming a unique set common to all lines the (co)variance matrices can be considered to be a good approximation. A similar result was obtained by Ragab and Baselga (2011) when comparing reproductive traits in the same four lines.

Table 7: Observed and expected differences between the effects of the line at foundation and at fixed times for slaughter weight (SW g).

		FOUNDATION				March 1997 - August 1998				June 2011 - September 2012			
	Contrast	**Mean[1]**	**SD[2]**	**$HPD_{95\%}$[3]**	**P>0[4]**	**Mean**	**SD**	**$HPD_{95\%}$**	**P>0**	**Mean**	**SD**	**$HPD_{95\%}$**	**P>0**
EXPECTED	**A-V**	70	38	-1 , 143	0.97	-6	8	-21 , 8	0.21	-6	8	-21 , 8	0.21
	A-H	-142	33	-207 , -73	0.07	-56	9	-73 , -39	0.00				
	V-H	-214	49	-309 , -126	0.00	-50	8	-66 , -34	0.00				
	A-LP	-217	34	-283 , -139	0.00					-56	9	-73 , -39	0.00
	V-LP	-372	57	-487 , -93	0.00					-50	8	-66 , -34	0.00
OBSERVED	**A-V**					-8	9	-25 , 8	0.17	-17	13	-43 , 8	0.09
	A-H					-59	10	-80 , -40	0.00				
	V-H					-51	9	-69 , -34	0.00				
	A-LP									-88	13	-114 , -62	0.00
	V-LP									-71	11	-92 , -50	0.00

[1]. Mean = Marginal Posterior Mean [2]. SD = Marginal Posterior Standard Deviation; [3]. $HPD_{95\%}$ = Marginal Posterior highest density region covering 95% of the density ; [4]. P>0 = probability of the difference being greater than zero.

A reduction, over time, from foundation to the fixed time of comparisons of the differences in growth traits (Tables 6, 7 and 8) between lines was observed, especially when comparing A and V animals with respect to H and LP. This reduction could simply be a consequence of considering different levels of the line-year-season factor for the calculation of the contrasts at the foundation and during the fixed time comparisons. Furthermore, this reduction might also be due to genetic change in the average of growth traits, either as consequences of selection for prolificacy in the different lines, unintentional selection for growth traits and (or) genetic drift. In order to estimate the contrasts at foundation of A and V lines with respect to H line, the year-seasons from June 1996 to August 1998 were considered, but in the fixed time comparison between the same three lines the years-seasons from March 1997 to August 1998 were taken into account (i.e. most of the years-seasons were common to both comparisons). Thus, for these particular contrasts (A-H and V-H) the hypothesis of reduction of the differences as a consequence of genetic change is the most likely cause. Lines A and V are those which are expected to show the stronger correlated response on growth traits since they were in fact selected over a longer period. However, this correlated response in lines A and V for growth trait after selection for NW is in disagreement with results by García and Baselga (2002b) for line V. They showed in the V line, by contemporary comparison of rabbits six generations apart, that there were no significant correlated responses on growth traits. In that the same study, the correlated response based on genetic trends was also calculated; in this case a slightly positive genetic response was observed both for WW and ADG.

Table 8: Observed and expected differences between the effects of the line at foundation and at fixed times for average daily gain (ADG g/d).

		FOUNDATION				March 1997 - August 1998				June 2011 - September 2012			
	Contrast	**Mean[1]**	**SD[2]**	**HPD$_{95\%}$[3]**	**P>0[4]**	**Mean**	**SD**	**HPD$_{95\%}$**	**P>0**	**Mean**	**SD**	**HPD$_{95\%}$**	**P>0**
EXPECTED	**A-V**	0.51	0.78	-0.99 , 2.02	0.75	-1.00	0.15	-1.30 , -0.72	0.00	-0.58	0.20	-0.99 , -0.19	0.00
	A-H	-3.99	0.77	-5.60 , -2.56	0.00	-1.82	0.17	-2.15 , -1.48	0.00				
	V-H	-4.19	1.12	-6.36 , -2.27	0.00	-0.82	0.16	-1.14 , -0.51	0.00				
	A-LP	-5.18	0.80	-7.34 , -3.71	0.00					-1.19	0.20	-1.58 , -0.80	0.00
	V-LP	-6.93	1.33	-9.54 , -4.80	0.00					-0.60	0.16	-0.94 , -0.30	0.00
OBSERVED	**A-V**					-0.87	0.18	-1.21 , 0.51	0.00	-0.44	0.28	-0.99 , 0.11	0.05
	A-H					-1.71	0.20	-2.09 , -1.30	0.00				
	V-H					-0.85	0.18	-1.18 , -0.47	0.00				
	A-LP									-1.18	0.27	-1.71 , -0.66	0.00
	V-LP									-0.74	0.22	-1.17 , -0.29	0.00

[1]. Mean = Marginal Posterior Mean [2]. SD = Marginal Posterior Standard Deviation; [3]. HPD$_{95\%}$ = Marginal Posterior highest density region covering 95% of the density ; [4]. P>0 = probability of the difference being greater than zero.

In addition to this, our results as well as those by García and Baselga (2002b), are in disagreement with Rochambeau (1998) who observed in the INRA 1077 line, which was selected for litter size, a reduction of WW with an important negative consequence in of decreasing the adult size of the does.

3.5 CONCLUSIONS

Important differences for growth traits were detected between the lines at fixed periods of time. These differences were in a large part similar to the differences estimated between the lines at their foundation, differences that are due to the processes and criteria used for the foundation of the lines. Therefore, all the issues related with the foundation of a new line should be carefully considered, and to base the foundation only on the factor of breed, without considering production criteria does not seem beneficial. The current differences between the performances of the lines were lower than the differences at their origin, probably because during selection for litter size at weaning these traits were genetically improved as well, either indirectly, after selection for prolificacy, by unintentional direct selection for growth and (or) by genetic drift. Strong agreement was exists between the current observed differences of the lines and their expected values. This result is evidence of the appropriateness of our genetic models.

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CHAPTER 4

Genetic analysis of growth traits in the progeny of rabbit does from a diallel cross.

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4.1 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 the fattening period between 28 and 63 d of age. The rabbits were the progeny of does from a full diallel cross between four maternal lines (A, V, H and LP) mated to bucks of the paternal line R. A total of 1,955 rabbits were measured during the complete fattening period and the traits were recorded weekly with the cage being the experimental unit for FI and FCR (283 cages). The rabbits of the sixteen genetic groups, corresponding to the type of does of the diallel cross, were distributed on four Spanish farms and one genetic group (V line) was present on all farms in order to connect records among them and to be used as a 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 g and 30 g, respectively). The observed differences in favor of A line for BW at weaning, were compensated at the completion of the fattening period (BW_{63}) respect to the other lines. During the whole fattening period, no significant differences were observed between 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 involved significance differences for FCR in

favor of H as sire line in HA and HL (AH-HA=0.22 and LH-HL=0.15, respectively). For all traits, the confidence intervals at 95% of all contrasts and effects were large. This means that there existed other relevant effects which could not be detected. The estimates of maternal heterosis were, in general, negative; this 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 poorest for all growth traits showing significant differences with the LP line for most of them, for instance 0.13 poorer FCR between 28 and 63 d. Grand-maternal effects were less important than direct-maternal ones.

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

4.2 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 and easier to measure and is moderately and negatively correlated with FCR (Piles et al., 2004a). Postweaning ADG has been traditionally used as selection criteria to indirectly improve FCR. These selection procedures exploit genetic variability within populations, in this case in 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 mainly produced following a three-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 (Brun, 1993; Brun and Saleil, 1994; Khalil et al., 1995; Orengo et al., 2003; Ragab, 2012).

Generally speaking, only reproductive or maternal traits are considered during the selection of the lines to be used in obtaining crossbred females; however, these females contribute 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 were from a full diallel-cross among four maternal lines and the sires from a paternal line.

4.3 MATERIAL AND METHODS.

4.3.1 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 since the beginning of the selection process for prolificacy until the present and were housed on the farm of the Animal Science Department, Universidad Politécnica de Valencia (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 Carlos de la Rápita, Tarragona). This line is now in its 22nd generation of selection.

Line A 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 breeds of rabbits 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 using a family index (Estany et al., 1989). Line V was established from four different synthetic populations in 1984. Selection candidates were 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 was 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 were selected from 25 – 30 % of the best evaluated matings, with a limit of 4 does by mating. The bucks were selected

within sire from the best mating of the sire to contribute a son to the next generation. Selection was done 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 Californian 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 were genetically evaluated exclusively based on their phenotype, i.e. individual selection. Each sire contributed a son to the next generation and does were selected weekly at a rate of around 20%, taking into account the average growth of the previous four weeks. Selection was in non-overlapping generations until the 25th generation.

In all the lines, does were mated for first time around 17 weeks of age and then serviced 10–12 days post-kindling and a pregnancy test was carried out by abdominal palpation on day 12 after 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).

4.3.2 Crossbreeding Design and Management

The study was carried out on four different farms, located in Altura (Castellón, Spain), Rioseco de Tapia (León, Spain), Valencia (Spain) and Sant Carles de la Rápita (Tarragona, Spain). On each farm, the same experimental design was performed. The distribution of the does on 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. The number of sires for each line was 25 and the majority of these sires were represented in the crossbreed dams.

Table1. Localizations of the genetic groups of the does

	Grand-dam line			
Grand-sire line	**A**	**H**	**LP**	**V**
A	UPV[1]	Altura	Rioseco[2]	Rioseco
H	Rioseco	San Carlos[3]	Rioseco	Altura
LP	Altura	Altura	UPV	Rioseco
V	Altura	Rioseco	Altura	ALL[4]

[1]. Universidad Politécnica de Valencia; [2]. Rioseco de Tapia; [3]. San Carlos de la Rápita; [4] .On all the farms

Twenty five females of 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). R line semen was used as pool of individual ejaculate; each one involved a minimum of 30 sires. 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. It was avoided that all animals in the same cage 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 five weeks 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 Carlos de la Rápita 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, and 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.

4.3.3 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**).

Body weight (**BW**, g) was measured at 28 ($\mathbf{BW_{28}}$), 42 ($\mathbf{BW_{42}}$) and 63 ($\mathbf{BW_{63}}$) days of age. These days correspond to the day of weaning, the end of the 2nd week of fattening, and the slaughter day, respectively. Individual average daily gain (**ADG**, g/d), FI and FCR were also calculated in addition to the overall fattening period ($\mathbf{ADG_{28\text{-}63}}$, $\mathbf{FI_{28\text{-}63}}$, $\mathbf{FCR_{28\text{-}63}}$) for the first 2 weeks of growth ($\mathbf{ADG_{28\text{-}42}}$, $\mathbf{FI_{28\text{-}42}}$, $\mathbf{FCR_{28\text{-}42}}$) as well as for the last 3 weeks of fattening ($\mathbf{ADG_{42\text{-}63}}$, $\mathbf{FI_{42\text{-}63}}$, $\mathbf{FCR_{42\text{-}63}}$).

In order to properly account for the number of live animals in a cage when computing FI, it was necessary to record the date of any deaths of young rabbit as well. In this analysis only data from live rabbits 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 analyzed ($FI_{28\text{-}42}$, $FI_{42\text{-}63}$ and $FI_{28\text{-}63}$) 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 two 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 was made 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 days). 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 seven days to the total number of rabbit-days, but it is assumed that dead rabbits do not consume for a few days prior to death. The number of days was 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 was between 100-200 g, 200-300 g or higher than 300 g it was assumed that during 2, 3 and 4 d, respectively, the rabbit had not eaten before death. Consequently a dead rabbit contributed 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:

$FI = -0.07x^2 + 6.02x + 53.17$, for Altura (Equation 1)

$FI = -0.05x^2 + 5.29x + 53.33$, for Rioseco de Tapia (Equation 2)

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

$FI = -0.04x^2 + 5.51x + 57.60$, for UPV (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 took 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 were calculated for each cage and period, the corresponding value for FCR was obtained by dividing the FI of the period by its ADG.

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

$$Y_{jkl} = GG_j + F_k + S_l + e_{jkl} \qquad \text{(Equation 5)}$$

Where: Y_{jkl} 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_l is the effect of the sex and e_{jkl} 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 VV animals were obtained by generalized 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 estimated 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 were obtained from a full diallel cross among four maternal lines, and their sires were of the same paternal R line. Thus, there were five 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 ($G_i^{M'}$, 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 could not be estimated individually; however, the following functions of them could 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 ≠ j, I = A, V, H, L and j = A, V, H, L (Equation 6)

b) Grand-maternal differences between lines, ($G_{i-j}^{M'} = G_i^{M'} - G_j^{M'}$) , i ≠ j, i = A, V, H, L and j = A, V, H, L (Equation 7)

c) Maternal heterosis, previously defined.

Estimable functions of the crossbreeding parameters were obtained (adjusting by generalized least-squares) as the estimates of the genetic groups effects (as contrasts to the V line) to the coefficients described in Table 2. In this generalized 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.

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

Estimable Function	**[1]AxA**	**AxL**	**AxH**	**AxV**	**LxA**	**LxL**	**LxH**	**LxV**	**HxA**	**HxL**	**HxH**	**HxV**	**VxA**	**VxL**	**VxH**
[2] G^{I}_{A-V}	1	0.5	0.5	0.5	0.5	0	0	0	0.5	0	0	0	0.5	0	0
G^{I}_{L-V}	0	0.5	0	0	0.5	1	0.5	0.5	0	0.5	0	0	0	0.5	0
G^{I}_{H-V}	0	0	0.5	0	0	0	0.5	0	0.5	0.5	1	0.5	0	0	0.5
[3] $G^{M'}_{A-V}$	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0
$G^{M'}_{L-V}$	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0
$G^{M'}_{H-V}$	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1
[4] H^{M}_{AL}	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
H^{M}_{AH}	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
H^{M}_{AV}	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
H^{M}_{LH}	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
H^{M}_{LV}	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
H^{M}_{HV}	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1

[1]. Genetic group, XxY; X= sire line of the doe; Y dam line of the doe; L=LP line; [2]. G^{I}_{X-V} : direct-maternal differences between line X and line V; [3]. $G^{M'}_{X-V}$: grand-maternal differences between lines X and V(see text for complete explanation); [4]. H^{M}_{XY} **:** maternal heterosis between lines X and Y.

4.4 RESULTS AND DISCUSSION.

4.4.1 Descriptive Statistics.

Summary statistics for all traits are shown in Table 3. The mean for slaughter weight (BW_{63}) is within the range of commercial weights in Spain (between 2000 and 2300 g). The raw average for FI_{28-63} was 127 g/d, this figure is lower than the mean of FI for the fattening period in Spain that is 135 g/d, but this average was obtained at a slaughter age of 66 days (MAGRAMA, 2012).

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

	[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.

For ADG and FCR, raw averages were 45.7 g/d and 2.79, respectively. For FCR, Carabaño (2000) reported a value of 3.2, but in this cited study the weaning day and slaughter age were not specified. Weaning weight (BW_{28}) raw averages were lower compared to the results from the same lines reported by Orengo et al. (2009), because in their study the rabbits were weaned at 32 days. However, BW_{63}, ADG_{28-63}, FI_{28-63} and

FCR_{28-63} were higher than in Orengo et al. (2009). On the one hand, the slaughter time in our experiment was 63 d, being 60 d in their study. In addition, 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 five diallel cross between three maternal and two 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 (BW_{63}, ADG_{28-63}, FI_{28-63} and FCR_{28-63}), perhaps because this study was made considering Caldes line (I.R.T.A), R line (U.P.V.) and their simple crossbreds, and both lines are paternal lines selected for growth traits (litter weight at weaning and individual daily weight gain between 32 and 60 days of age for Caldes line and daily gain between 28 and 63 d for R line, as previously explained).

4.4.2 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 (BW_{28}), differences were observed in favor of line A (significant with L and V). Orengo et al. (2004) reported that heavier 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 of kits 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). The V line kits were the lightest at weaning (significant with L), in this case differences in prolificacy (11.56 BA and 9.96 NW) cannot be used alone to explain weaning weight differences,

since line LP had higher prolificacy (12.30 BA and 10.56 NW) and also showed higher $BW_{28.}$

El Nagar et al. (2013) observed that V line produced less milk; and body weight at weaning has been shown to be associated with milk production (Lukefahr et al., 1983; McNitt and Lukefahr, 1990). During the fattening period (BW_{42}), the differences in favor of the line A decreased, but on the contrary, the difference of the V line with respect to the other lines were maintained (the contrasts A-V and LP-V remained significant in the same direction). At the end of the fattening period, the differences in favor of A line for BW_{28} were compensated, and, finally, BW_{63} for lines H and LP were the highest. It seems that some form of compensatory growth took place after weaning; this process has previously been shown in rabbits by Testik et al. (1999) and Belhadi (2004). This result is in agreement with those by Mínguez et al. (2012), who showed that H and LP lines were the heaviest at foundation and also at present after the selection process. The relationship between BW, ADG and FI during the whole fattening period can be observed in Table 4. If the difference of a contrast between BW_{28} and BW_{63} was reduced, the sign of the corresponding contrast for $ADG_{28\text{-}63}$ was negative, being positive when the difference of the contrast between BW_{28} and BW_{63} was increased. An increase of 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, mainly during the last part of the fattening $FCR_{42\text{-}63}$, but also for the whole fattening period $FCR_{28\text{-}63}$.

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

	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 $\alpha = 0.05$).

For A and V lines, we obtained similar results for $BW_{28,}$ FCR_{28-42} and FCR_{28-63} as Feki et al. (1996) who showed superiority of the line A over line V for $BW_{28,}$ and no significant differences in FCR_{28-42} and FCR_{28-63}. However, for ADG_{28-42}, ADG_{28-63}, FI_{28-42} and FI_{28-63} they showed a superiority of line V, although superiority was not confirmed in our study.

Although no significant differences were observed during the whole fattening period for all growth traits, it should be taken into account the great width of the confidence intervals at 95%. 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 BW_{63} (contrast A-H), -3.3 g/d for ADG_{28-63} (contrast A-H), 12 g/d for FI_{28-63} (contrast LP-V) and 0.20 for FCR_{28-63} (contrast A-H). The magnitudes of these figures are expected to have important economic consequences.

On commercial farms, crossbred does are the most common type of females and, consequently, some differences for growth traits due to 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 (BW_{28}), once again these results could partially be explained by differences due to 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. However, this explanation does not hold for AV crossbred does which had higher BA than V does. In this case, the significant difference in favor of the AV is perhaps due to the, aforementioned, lower milk production of the V line.
It could be expected that the crossbred dams would show better performance than line V maternal-reared animals. However, as occurred 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 appeared to be compensated during the whole fattening period. In this sense it can be noted that the crosses that had advantage over the line V for BW_{28} had a subsequent growth rate that was slower than the V line. Such is also the situation when crossbreds are considered together (All-VV). As happened for lines, it seems that the compensatory growth also appeared for the contrasts between crosses.

This compensatory growth is expected because maternal effects lose importance after weaning (Mínguez, 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 ADG_{42-63} was opposite to that for ADG_{28-42}, being that all the estimates for the latter were positive but only significant for the contrast AL-VV.

Contrarily to the contrasts between lines, during the first two weeks and the last three weeks of fattening, was common that a given contrast between a couple of crossbreds for FI and the corresponding contrast for ADG had different sign. This result could explain the observed significant contrasts for FCR during the first two weeks and the last three weeks of fattening, but the most important factor determining the results for FCR seems to be linked to ADG. Thus, of practical value, 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 FCR_{28-42} were all significantly positive except for HV-VV and LV-VV. On the contrary, the contrasts for FCR_{42-63} 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

$FCR_{28\text{-}63}$ became non-significant. The confidence intervals at 95% were large for the contrasts between crossbred genetic groups and for the V line as occurred in the comparison between the lines. This means that relevant differences due to other factors 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

Table 5. Contrasts (standard error) between crossbred genetic groups[1] and V line for body weight ([2]**BW**, g), average daily gain ([3]**ADG**, g/d), individual feed intake ([4]**FI**, g/d) and feed conversion ratio ([5]**FCR**).

	[1]AH-VV	AL-VV	AV-VV	HV-VV	LH-VV	LV-VV	All-VV
$\mathbf{BW_{28}}$	26(10)*	44(10)*	31(10)*	6(10)	15(10)	11(10)	22(8)*
$\mathbf{BW_{42}}$	-12(19)	4(19)	-5(19)	6(19)	3(20)	-10(20)	-2(15)
$\mathbf{BW_{63}}$	-22(26)	28(26)	2(27)	-2(26)	28(26)	-6(27)	4(20)
$\mathbf{ADG_{28\text{-}42}}$	-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)*
$\mathbf{ADG_{42\text{-}63}}$	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)
$\mathbf{ADG_{28\text{-}63}}$	-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)
$\mathbf{FI_{28\text{-}42}}$	0(2)	1(2)	-1(2)	0(2)	4(2)*	-1(2)	1(2)
$\mathbf{FI_{42\text{-}63}}$	-3(3)	-2(3)	-1(3)	-1(3)	-0(3)	-6(3)*	-2(2)
$\mathbf{FI_{28\text{-}63}}$	-2(2)	-1(2)	-1(2)	-1(2)	1(2)	-4(2)	-1(2)
$\mathbf{FCR_{28\text{-}42}}$	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)*
$\mathbf{FCR_{42\text{-}63}}$	-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)*
$\mathbf{FCR_{28\text{-}63}}$	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.] $ADG_{x\text{-}y}$, average daily gain between days x and y; [4.] $FI_{x\text{-}y}$, individual feed intake between days x and y per day; [5.] $FCR_{x\text{-}y}$, 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 $\alpha = 0.05$).

BW_{63} (contrast LH-VV), -2.1 g/d for ADG_{28-63} (contrast AH-VV), 9 g/d for FI_{28-63} (contrast LV-VV) and 0.09 and -0.09 for FCR_{28-63} (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). Although for a given cross and its reciprocal were raised on different farms (Table 1), they were connected by the line V that was raised on all the farms. The consequence of this is that the standard 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 with respect to line V (Table 5). Despite the large errors, significant differences for the contrast AL-LA, being in favor of LA, were observed for weaning weight (BW_{28}). The effect on pre-weaning growth of the size of the litter 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), although it should be noted that this last comparison showed a significantly higher ADG_{42-63} than the LA cross, inverting the sign of the corresponding contrast for ADG_{28-42}. So, here appeared a manifestation of compensatory growth, phenomenon also presented and commented for the pure lines . It is also important to note that the contrast AH-HA was significant for FCR_{28-42} (0.30±0.08) and FCR_{28-63} (0.22±0.07), being that the differences was in favor of that cross in which the A line acts as the dam and line H as the sire. Similarly, the contrast between LH and HL was also favourable for FCR_{28-63} (0.15±0.07) in the cross where H line acts as the sire. The criteria of foundation of the H line based on hyperprolificacy (García-Ximénez et al., 1996) might explain why the H line is preferred to be used as

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

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 $\alpha = 0.05$).

the sire. As a higher prolificacy line provides a poorer maternal environment (i.e., more competition among siblings), the hyperprolificacy of the H line as dam would penalize 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 FCR_{28-42} a significantly favorable effect (-0.21±0.08) in using the V line as sire was observed. This result could also be related to the foundation in the V line, which carried out through integrating four populations noted for their high prolificacy. In the significant contrasts for FCR_{28-63}, given the high estimation errors, the maximum values that the 95% confidence interval yields could reach 0.36 and 0.29; whereas, 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 from a practical standpoint. In disagreement, 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 done from a productive point of view, and a number of contrasts with applied interest have 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 however low, after taking FCR into account. Therefore, despite the fact

that, in general, no significant differences were observed between lines, neither between crosses and the V line nor between reciprocal crosses for $FCR_{28\text{-}63,}$ the biological differences could be relevant to this important economic trait.

4.4.3 Direct-maternal effects.

Differences between direct-maternal effects are shown in Table 7. At weaning, significant differences for the contrast G^{I}_{A-V} and G^{I}_{L-V} 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 $ADG_{28\text{-}42}$, 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 three weeks of the fattening, becoming significantly inferior to the H and V lines for $ADG_{42\text{-}63}$. The higher direct-maternal effect of the LP line on $ADG_{28\text{-}42}$ was parallel to a similar effect on $FI_{28\text{-}42}$. However this parallelism was not evident in the last three weeks of fattening. Regarding FCR, there were no significant differences during the first two weeks, despite the observed differences mentioned previously for ADG and FI. FCR that showed significant differences in the contrasts G^{I}_{L-V} and G^{I}_{A-V} , favorable in both cases for the V line. In the contrast G^{I}_{L-V} , significant differences were also observed for the entire fattening period. The general positive effect associated with line V on FCR is probably related to the lower means for body weights of line V; as is well known, FCR increases with body weight within genetic types (Torres et. al, 1992; Feki et al., 1996; Sánchez et al., 2004).

During the whole fattening period, in addition to the previously mentioned significant effect for $FCR_{28\text{-}63}$, the only observed significant differences were found for BW_{63} and $FI_{28\text{-}63}$. Also, the contrast G^{I}_{L-V} , now favored the LP line. This result partially agrees

Table 7. Direct-maternal differences between lines[1] (standard error) for body weight ([2]**BW**, g), average daily gain ([3]**ADG**, g/d), individual feed intake ([4]**FI**, g/d) and feed conversion ratio ([5]**FCR**).

	[1] G^I_{A-H}	G^I_{A-L}	G^I_{A-V}	G^I_{H-V}	G^I_{L-H}	G^I_{L-V}
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_{i-j} , 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 $\alpha = 0.05$).

with results by Mínguez et al. (2011), where fryers in the LP line were 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 BW_{63}, ADG_{28-63}, FI_{28-63} and FCR_{28-63}, who did not find any relevant differences. The only disagreement with Orengo et al. (2009) concerns BW at weaning, in which we observed significant differences, but their study involved weaning at 32 d instead of 28 d as in our study.

After studying direct-maternal effects (Table 7), as a general result, it can be shown that V line was the poorest of all lines for 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 highest values for the contrast between lines for direct-maternal differences. However, the agreement is not complete because the importance of the grand-maternal effects of the lines that 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 were perfect, i.e. there was no error, the contrast between lines, for example A and V would be: AA-VV= $G^{I}_{A-V} + G^{M'}_{A-V}$, according to Table 2.

4.3.4 Grand-maternal effects.

Grand-maternal effect differences between lines are shown in Table 8. Comparisons of the standard errors of the corresponding contrasts for direct-maternal effects (Table 7) and grand-maternal effects show that the errors for the latter are between 50% and 80%, being smaller than those for the former, which suggest 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 may be lower than the importance of the latter.

Significant differences for grand-maternal effects in BW_{28} have not been found. The number of kits weaned is a trait closely related to BW_{28}, for this trait Ragab (2012) did not find any significant difference on maternal genetic effects using the same set of crossbred does. This result is consistent 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 weaning of their daughters (maternal effect) or the weaning weight of their grand-progeny (grand-maternal effect). There were significant differences in BW_{42}, favorable to the V line, for the contrasts $G^{M'}_{A-V}$ and $G^{M'}_{L-V}$. This result is opposite to the estimates obtained for direct-maternal effects. In addition, line V maintained its favorable grand-maternal effect with respect to line LP until the end of the fattening period (BW_{63}). During the first two weeks of fattening, the effects of line V as grand-dam on ADG were significantly higher than those of the other lines but only during the last three weeks A line showed a superior effect as grand-dam, over this period the V line was the poorest. Because of this change in the effects between the two 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 three weeks of fattening showed a significant effect not in favour of this line. In the first two weeks the same contrasts showed an opposite sign, being significant between the H line. Thus, similar to results for ADG, the contrasts regarding the grand-maternal effect for FCR during the two periods tended to compensate each other resulting in no significant observed differences for the entirefattening period ($FCR_{28\text{-}63}$).

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

	[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)*
$ADG_{28\text{-}42}$	-1.5(1.0)	-1.8(1.1)	-4.2(1.2)*	-2.7(1.0)*	0.3(1.0)	-2.4(1.1)*
$ADG_{42\text{-}63}$	1.9(0.8)*	2.9(0.9)*	3.6(1.0)*	1.7(0.8)*	-1.0(0.8)	0.7(0.9)
$ADG_{28\text{-}63}$	0.7(0.7)	1.2(0.8)	0.3(0.8)	-0.4(0.7)	-0.3(0.7)	-0.9(0.8)
$FI_{28\text{-}42}$	-2(2)	-3(3)	-5(3)	-2(3)	0(3)	-2(3)
$FI_{42\text{-}63}$	-3(4)	2(5)	-6(5)	-2(4)	-6(4)	-8(5)
$FI_{28\text{-}63}$	-3(3)	0(3)	-5(4)	-2(3)	-3(3)	-6(3)
$FCR_{28\text{-}42}$	-0.02(0.05)	0.02(0.06)	0.13(0.07)	0.11(0.05)*	0.00(0.05)	0.10(0.06)
$FCR_{42\text{-}63}$	-0.12(0.07)	-0.09(0.08)	-0.33(0.09)*	-0.20(0.07)*	-0.04(0.07)	-0.24(0.08)*
$FCR_{28\text{-}63}$	-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]. $ADG_{x\text{-}y}$, average daily gain between days x and y; [3]. $FI_{x\text{-}y}$, individual feed intake between days x and y per day; [4]. $FCR_{x\text{-}y}$, feed conversion ratio between days x and y; L:LP line;

*$P < 0.05$ (significant difference at $\alpha = 0.05$).

4.3.5 Maternal heterosis.

Estimates of maternal heterosis effects are shown in Table 9. A result which clearly draws attention is that the sign of the majority of the estimates for BW, ADG and FI are negative. This could be a partial consequence of the positive heterosis expressed 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 penalize 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 estimates involving the line A, which is the line with the lowest prolificacy (Ragab and Baselga, 2011), were more frequently significant particularly for the combinations AH and AL. The combination of lines A and H was the most important, bearing negative and significant heterosis effects. This result could be related to the low prolificacy of line A, already noted, and with the result that the cross AH showed a significant positive heterosis for the total number of kits born (Ragab, 2012). The estimates of the heterosis for FCR were also negative, particularly for the last part of the fattening period, which were significant for AH and AL, in this case negative values that were favourable. These favourable heterotic effects on FCR at the end of the fattening period are probably related to the negative maternal heterosis on BW63, representing a reduction of slaughter BW in crossbred offspring, which, as already stated, reduces FCR (Torres et. al, 1992; Feki et al., 1996; Sánchez et al., 2004). Actually, we have also performed the analysis using number born alive as covariate. The corresponding regression coefficients were always negative, as expected. The estimates were significant and around -22 g/rabbit for weight traits; significant and

around -0.25 g/d.rabbit for daily gain traits; significant and around -0.80 g/d.rabbit for daily feed intake traits and non-significant and around -0.013/rabbit for food conversion traits. However, regarding the maternal heterosis, the conclusions obtained with this analysis are essentially similar to those obtained in the analysis without covariates. Other results that deserve attention are the favourable heterosis effect for ADG_{42-63} between lines LP and V, together with the significantly positive and unfavorable heterosis for FCR_{28-42} between lines H and V.

In this work, the design of the experiment did not allow for an estimation of direct heterosis effects which could be related to genes affecting growth, which are expected to be small. 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, maternal heterosis expressed in percentage was small, being inferior or equal to 6%.

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

	[1] H_{AH}^{M}	H_{AL}^{M}	H_{AV}^{M}	H_{HV}^{M}	H_{LH}^{M}	H_{LV}^{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}	-2	-1	-1	-1	0	-1
$ADG_{28\text{-}42}$	-3.5(1.0)*	-2.9(1.1)*	-0.9(1.0)	-0.8(0.8)	-0.3(0.9)	-1.1(0.8)
$ADG_{42\text{-}63}$	1.1(0.8)	1.3(0.9)	-0.0(0.8)	-0.1(0.7)	0.0(0.7)	1.4(0.7)*
$ADG_{28\text{-}63}$	-0.7(0.7)	-0.3(0.7)	-0.3(0.7)	-0.7(0.6)	-0.2(0.6)	0.2(0.6)
%, $ADG_{28\text{-}63}$	-2	0	-1	-1	0	0
$FI_{28\text{-}42}$	-5(2)*	-1(3)	-1(2)	3(2)	2(2)	-2(2)
$FI_{42\text{-}63}$	-9(4)*	-6(5)	-5(4)	-5(3)	-6(3)	-5(3)
$FI_{28\text{-}63}$	-7(6)*	-4(3)	-3(3)	-2(2)	-4(2)	-4(2)
%, $FI_{28\text{-}63}$	-6	-3	-3	-2	-3	-3
$FCR_{28\text{-}42}$	0.07(0.05)	0.11(0.06)	0.00(0.05)	0.15(0.04)*	0.03(0.04)	0.04(0.04)
$FCR_{42\text{-}63}$	-0.15(0.07)*	-0.23(0.08)*	-0.06(0.07)	-0.03(0.06)	-0.09(0.06)	-0.06(0.06)
$FCR_{28\text{-}63}$	-0.04(0.04)	-0.07(0.05)	-0.04(0.04)	0.03(0.04)	-0.04(0.04)	-0.02(0.03)
%, $FCR_{28\text{-}63}$	-1	-2	-1	1	-1	0

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

4.5 CONCLUSIONS

Few significant differences between lines, crosses and V line, and between reciprocal crosses 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 through 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 economically 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, following Dickerson's model, similar patterns of effects to those obtained in the comparison between lines and crosses were obtained. 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 large litter sizes.

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CHAPTER 5

Genetic analysis of slaughter and carcass quality traits in crossbred rabbits from a diallel cross of four maternal lines.

5.1 ABSTRACT

An experiment was carried out to estimate the genetic group effects and the crossbreeding genetic parameters for slaughter and carcass traits using data from rabbits that were progeny of does from a full diallel cross between four maternal lines (A, V, H and LP) mated to bucks of the paternal line R. The rabbits of the sixteen genetic groups, corresponding to the type of does of the diallel cross, were distributed on four Spanish farms with one genetic group (V line) being present on all farms in order to connect records among them and to be used as reference group. Crossbreeding parameters were estimated according to Dickerson's model. A total of 1,896 rabbits were measured for slaughter traits and 950 for carcass traits. The averages values for all the traits were within the range in the bibliography consulted. The A and LP lines had the lowest values for dressing percentage (-1.71 and -1.98 compared with H line and -1.49 and -1.75 with the V line, respectively). The A line was the heaviest for commercial carcass weight (differences of 83 g compared with the line H and 60 g with the V line). No relevant differences were observed between the crossbred groups for all traits. Regarding the reciprocal effects, there were significant differences in favor of A line as sire line in the crossbred AV (with differences of 99, 26 and 27 g for cold carcass, hind leg and loin weights, respectively). Regarding the combination of direct and maternal effects, the A line showed significantly higher values for cold carcass weight than any other line (133 , 71 and 142 g with respect to the H, LP and V lines). For the same parameter, the H line showed significantly higher averages for dressing

percentage than A and LP lines, values of 1.44 and 2.13%, respectively. Also A line showed, in general, better direct-maternal effects than V line. Grand-maternal effects were less important than direct-maternal ones, but in this case, this effect reached significance for cold carcass weight in the comparisons between A line and any other line. The estimates of maternal heterosis were, in general, negative. This could be a consequence of positive heterosis for litter size. However, despite this relationship between growth and litter traits, it has not been common to find negative maternal heterosis for growth traits.

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

5.2 INTRODUCTION.

In general, meat production in rabbits is based on a three-way crossbreeding scheme that utilizes maternal and paternal lines. The selection criteria for maternal lines are litter size at birth or at weaning (Rochambeau et al., 1994, Garreau et al., 2004), while the paternal lines are selected for growth traits (Baselga, 2004). The selection for growth traits has reduced the growing period, because carcass weight is fixed by the market, so the degree of maturity of rabbits is lower (Pascual, 2007). At present, the slaughterhouses are tending to pay incentives for higher dressing percentage but the decrease of the degree of maturity produces a reduction of values for this trait (Parigi-Bini et al., 1992, Dalle-Zotte and Ouhayoun, 1995; Lebas et al., 2001).

Presently, 80% of the marketing of rabbit meat in Spain is based on the whole carcass (Montero, 2011), but it is necessary to offer news products (e.g. cut parts) for the expansion of the production (Dalle Zotte, 2002). Carcass quality research is

increasing in importance because the consumer demands leaner carcasses, attractive and implicitly wholesome. Fortunately, the commercial rabbit carcass is quite lean and does not present serious qualitative problems linked to anomalies of muscle biology or to the pre- and post-slaughter handling, compared to other species like pigs (Ouhayoun, 1992). Carcass quality can be also defined as the proportion of cut parts such as loin, hind and fore part (Larzul and Gondret, 2005). Another criterion defining carcass quality is the meat/bone ratio of the carcass, which can be fairly well predicted by the hind leg meat/bone ratio (Blasco et al., 1992). Also, carcass and muscle colour of the cuts are traits that are now more relevant as they might affects consumer acceptance and purchasing decisions. Rabbit meat is paler than pork or beef with a low redness index (Hernández et al., 1997).

The objective of this work was to estimate differences and crossbreeding parameters for slaughter traits and carcass quality of rabbits, whose dams come from a full diallel-cross among four maternal lines and the sires from a paternal line, with all the lines derived from a large Spanish program promoting genetic improvement.

5.3 MATERIAL AND METHODS.

5.3.1 Animals.

The present study involved animals, whose dams came from a full diallel cross among four maternal lines (A, V, H and LP) and their sires were from a 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 used for this study were a sample of the animals used in Chapter 2.

5.3.2 Crossbreeding Design and Management.

The study was carried out on four different farms located in Altura (Castellón, Spain), Rioseco de Tapia (León, Spain), Valencia (Spain) and Sant Carles de la Rápita (Tarragona, Spain). On each farm, the same experimental design was performed. The distribution of the does on the farms was shown in Chapter 2. The genetic group VV was present on all farms allowing data connection across farms, but because this was the only genetic type found on all the farms no interaction between farm and genetic type could be considered.

Twenty-five females of 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 into collective cages of eight individuals until marketing at 63 d of age. It was avoided to have all animals in the same cage that belonged to the same litter, but they always belonged to the same genetic group. During the post-weaning period, rabbits were fed *ad libitum* on a standard commercial pellet diet and fresh water.

The whole fattening period lasted five weeks on all the farms. On the farm of Altura data collected took place from February 1st 2011 to March 8th 2011; on Rioseco de Tapia from May 9th 2011 to June 13th 2011; on UPV from February 21st 2012 to March 27th 2012, and on San Carlos de la Rápita 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 mortality was unequal across genetic groups, thus the distribution of animals by genetic group was unbalanced. The observed high mortality could have been the consequence of the intense weekly manipulations of young rabbits used for collecting data.

The rabbits were fasted of pelleted feed for 24 hours before slaughter. The transport of the rabbits to the slaughterhouse was in an adapted vehicle, authorized to perform the activity. The commercial slaughterhouse for animals from the farm of Altura was located in Gaibiel (Castellón, Spain). For the rest of the animals, slaughter was conducted in the experimental slaughterhouse of the Animal Science Department of the Polytechnic University of Valencia (UPV). In all cases, the journey was less than 12 hours, including loading and unloading of the animals. In the loading of rabbits, the genetic groups were randomized (each box contained one animal from each genetic group) to avoid differences due to waiting times at the slaughterhouse. Spanish legal protocols (BOE-A-1995-3942) call for stunning by electrical shock to prevent animals from suffering. In both slaughterhouses, an electrical shock with a voltage and frequency of 49 V and 179 Hz, respectively, and with duration of two seconds, approximately, was used. The electrical shock that also involved immobilizing the animal to facilitate the initiation of bleeding was needed to preserve the safety of personnel, and to ensure the desired development of muscle to meat (Ouhayoun, 1988).

5.3.3 Data Recording and Statistical Model.

All the slaughter and carcass traits studied followed the official criteria and terminology of the World Rabbit Scientific Association. For more information of the specificities about these traits see Blasco et al. (1993). The slaughter traits studied were: Live weight at 63 days (after fasting, **LW63**, g.), commercial skin weight (**CSkW,** g.),

full gastrointestinal tract weight (**FGTW**, g.), hot carcass weight (**HCW**, g.), and dressing percentage (HCW divided by LW63 x 100, **DP**). These traits were measured in the slaughterhouse.

After slaughter, hot carcasses were chilled for 24 h at 4°C and carcass quality characteristics were measured in the meat laboratory of the Department of Animal Science of the UPV. The carcass colour in the CIELAB space (***L*, a**** and ***b****) was recorded on loin surface at the 4th lumbar vertebra of the right side at 24h post-mortem using a CR300 Minolta Chromameter. The commercial carcass weight was recorded (**CCW**, g.) and then carcasses were dissected and measured according to the norms of the World Rabbit Scientific Association. Head weight (**HW**, g.), liver weight (**LvW**, g.), whole thoracic viscera weight (lungs, thymus, oesophagus, heart, **LHW**, g.) and kidneys weight (**KiW**, g.) were recorded in these carcasses. All of these parts were removed to obtain the reference carcass weight (RCW, g.).Reference carcass contained only meat, fat, and bone. Scapular (**SFaW**, g.) and perirenal fat (**PFaW**, g.) were excised from the carcass and were weighted. The technological joints measured were: fore leg weight (**FLW**, g.), thoracic cage weight (without the insertion muscles of fore legs, **TW**, g.), loin weight (**LW**, g.) and hind leg weight (**HLW**, g.). From the hind part of the carcass, the left leg was then dissected to separate bone from edible meat to calculate meat to bone ratio (**M/B**).

A total of 1896 carcasses were used to measure the slaughter traits and a sample of 950 carcasses were used in the meat laboratory (50 carcasses for each genetic group and farm) for measuring carcasses quality traits, with the exception of M/B for which a subsample of 475 carcasses (25 left legs for each genetic group and farm) were recorded.

The model used in the analysis was:

$$Y_{jkl} = GG_j + F_k + S_l + e_{jkl}$$

Where Y_{jkl} 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_l is the effect of the sex and e_{jkl} is the residual effect.

Estimates of the differences between all the genetics groups and VV animals were obtained by generalized least-squares, using the program blupf90 (Misztal et al., 2002). In addition to the estimates, the error (co)variance matrix between these estimates was obtained. The residual variances required to solve the models were estimated from 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 different genetic groups.

Given the genetic make-up of the experimental animals there were five 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 ($G_i^{M'}$, 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 are not estimable individually, but the following functions of them are estimable:

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 ≠ j, i = A, V, H, L and j =A, V, H, L

b) Grand-maternal differences between lines, ($G_{i-j}^{M'} = G_i^{M'} - G_j^{M'}$), i ≠ j, i = A, V, H, L and j=A, V, H, L

c) Maternal heterosis, previously defined.

Estimable functions of the crossbreeding parameters were obtained, being adjusting by generalized least-squares, to provide the estimates of the genetic groups effects (as contrasts to the V line) to the coefficients described in Chapter 2. In this generalized 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 of both contrasts between genetic types and estimable functions of the crossbreeding genetic parameters.

5.4 RESULTS AND DISCUSSION.

5.4.1 Descriptive Statistics.

Summary statistics for all traits are shown in Table 1. For slaughter traits, the mean for LW63 and HCW is within the range of commercial weights in Spain (2100 and 1200 g, respectively) (MAGRAMA, 2012). Pla (2008) studied animals from a three-way crossbreeding scheme (Rx(AxV)) and slaughtered them also at 63 days. He obtained superior average values for all measured traits; only DP (%) showed a lower average than in our study. This superiority can be explained because all the animals in the Pla (2008) study were fattened at the experimental farm of the UPV with different environmental conditions. For A, V and R lines as purebred, Hernández et al. (2006) and Zomeño et al. (2010) obtained general averages for these traits similar to ours.

Gómez et al. (1998) studied, at a fixed age of 60 days, some slaughter and carcass traits and the averages obtained for them also being in the same magnitude as in our

study; they considered purebred animals from the maternal lines Prat and V and from the paternal lines Caldes and R. Prat and V lines were selected for litter size at weaning (the V line was explained above), and Caldes and R line were selected for individual post-weaning daily weight gain. The similarities between our study, and the studies of Hernández et al. (2006) and Gómez et al. (1998) were expected because they used purebred animals and the overall average was the average between the paternal and maternal lines. We only obtained superior values compared to studies by Hernández et al. (2006) and Zomeño et al. (2010) for SFaW and PFaW, this is because we used the line R as parent for all young rabbits and it has been shown (Hernández et al., 2004) that the R line have higher dissectible fat than the lines A and V. Piles et al. (2004) only used the paternal lines R and Caldes and their overall mean for LW63, CCW and DP were clearly superior to ours.

Table 1. Descriptive statistics for slaughter and carcass quality traits.

Trait[1]	N[2]	Mean	SD[3]	Minimum	Maximum
LW, g	1896	2144	234	1200	2880
CSkW, g	1896	232	35	110	385
FGTW, g	1896	404	51	280	630
HCW, g	1896	1250	154	650	1650
DP, %	1896	58	2	50	63
L*	950	56.81	2.5	47.43	63.87
a*	950	3.59	1.17	0.58	8.51
b*	950	-0.12	2.30	-7.9	5.74
CCW, g	950	1249	144	750	1638
HW, g	950	116	11	81	154
LvW, g	950	77	18	42	148
KiW, g	950	15	1	8	27
LHW, g	950	27	4	14	46
RCW, g	950	1013	130	563	1361
SFaW, g	950	7	2	1	16
PFaW, g	950	19	6	4	59
HLW, g	950	380	46	227	532
LW, g	950	317	49	109	463
FLW, g	950	174	25	94	248
TW, g	950	107	19	51	200
M/B	475	5.0	0.6	2.9	6.4

[1] . LW63= liveweight at 63 days after fasting, CSkW= commercial skin weight, FGTW= full gastrointestinal tract weight, HCW= hot carcass weight, DP= dressing percentage, L*= lightness of loin surface, a*= redness of loin surface, b*= yellowness of loin surface, CCW= commercial carcass weight, HW= head weight, LvW= liver weight, KiW= kidneys weight, LHW= thoracic viscera weight, RCW= reference carcasses weight, SFaW= scapular fat weight, PFaW= perirenal fat weight, HLW= hind leg weight, LW= loin weight, FLW= fore leg weight, TW= thoracic cage weight, M/B= meat to bone ratio, [2]. N= number of rabbits, [3]. SD= standard deviation.

5.4.2 Differences between genetic groups.

In Tables 2 and 3, the contrasts between the dam effects of the lines for the studied traits can be observed. Differences in LW63 are economically important because the income of farmers are realized by LW63. It can be observed that V line had the lightest and the LP line had the heaviest mean values (no significant differences for this trait). The result for V line is in agreement with Mínguez et al. (2012), who showed that at 63 days, the H and LP lines were the heaviest, followed by the A line, and the V line was the lightest. For the contrast A-V, Hernández et at. (2006) obtained the same result. For CSkW, the A and LP lines were the heaviest with significant differences with respect to the V line (the lightest one). This result is in agreement with Pla et al. (1995) who found that the skin of the line A was heavier than that for the line V. For DP, the lines A and LP showed the lowest mean values, with significant and relevant differences with respect to the lines H and V. It has to be noted that in spite of the low variability of the character, s.d. equal to 2 %, differences between lines of up to 1.98% were observed. With respect to HCW, the superiority observed for CSkW of the A and LP lines, which also showed the heaviest LW63, either caused the observed differences between lines to be reduced or changed the sign of the differences in LW63.

This reduction also affected the contrasts A-V and LP-V regarding DP to be of opposite sign to those for LW63. It was observed that, when the contrasts for CSkW had the same sign as those for LW63 that significant differences in DP were observed, i.e. the differences between LW63 and HCW were higher. Note that the significant differences in DP were between the heaviest and the lightest lines for LW63 and CSkW (contrasts A-H, A-V, LP-H and LP-V). The differences in favor of A and LP lines for FGTW, as previously mentioned for the CSkW, may also contribute to reduce the DP of these

lines, although the differences for this trait were less important. This agrees with the results by Ouyed et al. (2011), for Californian, American Chinchilla and New-Zealand White breeds; they observed that the rabbits with the lowest LW63 also had the highest DP. They explained this result by the lower proportion of skin found in these rabbits.

Most rabbit meat is usually commercialized as whole carcasses, but presently retail cuts are increasing in importance. No significant differences were observed for L*, but for a* and b*, the V line showed the lowest values (with significant differences with the other lines). These results are in agreement with Hernández et al. (2006), who obtained small differences for L* between lines A and V, but rather relevant differences regarding a* and b*. Dalle Zotte and Ouhayoun (1998) also found differences for L*, a* and b* between different rabbit breeds. At present, consumers do not seem to have preferences for colour carcass, but it would be convenient to survey possibles changes in colour traits along the selection program for other traits (Hernández et al., 2006).

Table 2. Contrasts (standard error) between the lines for slaughter and carcass colour traits.

Trait[1]	A-H	A-LP	A-V	H-V	LP-H	LP-V
LW63, g	28(76)	-40(54)	53(54)	25(53)	68(77)	93(56)
CSkW, g	10(10)	3(7)	23(7)*	13(7)	6(10)	19(7)*
FGTW, g	15(15)	-8(10)	10(10)	-5(10)	23(15)	18(11)
HCW, g	-25(48)	-19(35)	-5(35)	19(34)	-6(49)	13(35)
DP, %	-1.71(0.60)*	0.24(0.43)	-1.49(0.43)*	0.22(0.42)	-1.98(0.43)*	-1.75(0.44)*
L*	-0.09(0.59)	-0.38(0.45)	-0.27(0.43)	-0.18(0.42)	0.30(0.56)	0.12(0.41)
a*	-0.03(0.25)	0.13(0.18)	-0.53(0.18)*	-0.51(0.18)*	-0.15(0.36)	-0.66(0.18)*
b*	-0.07(0.48)	-0.26(0.35)	-1.08(0.35)*	-1.00(0.33)*	0.19(0.48)	-0.82(0.34)*

[1] . LW63= liveweight at 63 days after fasting, CSkW= commercial skin weight, FGTW= full gastrointestinal tract weight, HCW= hot carcass weight, DP= dressing percentage, L*= lightness of loin surface, a*= redness of loin surface, b*= yellowness of loin surface. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

For CCW the line A was the heaviest (with significant differences with H and V lines). Despite that the correlation between HCW and CCW that is near one (Ogah et al., 2012), the contrasts between the lines for HCW change the sign for CCW. This change between HCW and CCW can be a random consequence because the animals measured in the laboratory were also a sample of the animals used for measuring slaughter traits (50% aprox.). For HW, the line A was the heaviest (significant differences with H and V lines) followed by the LP line (significant differences with V line) and the V line was the lightest. These results do not agree with results by Gómez et al. (1998) that used Prat, Caldes, R, V and A lines; they did not find any differences between the lines for this trait. There were some significant differences for LvW (H-V in favor of the H line) and KiW (A-H and A-V in favor of the A line) but they are not economically relevant. For LHW no significant differences were found. These results are in agreement with Gómez et al. (1998) who compared these traits for A and V lines. For reference carcass weight (RCW), the line A was the heaviest, with significant differences with respect to H and V lines. The reference carcass weight (RCW), as defined by Varewyck and Bouquet (1982), contains only fat, meat and bone tissues. RCW and CCW are directly related as RCW is equal to CCW plus HW, LvW, KiW and LHW, and because the differences between lines for HW, LvW, KiW and LHW are small, RCW contrasts were significant in the same cases as those for CCW. Rabbit carcasses have a small dissectible fat percentage (Pla et al., 1996). Scapular and perirenal fat tissues are two of the main depots of the carcass and correspond to 65% of the carcass dissectible fat in the rabbit (Hernández et al., 2006; Zomeño et al., 2010). For the contrasts between lines for SFaW, the H line was the heaviest and the V line was the lightest, being significant the difference between them. Regarding PFaW, the A line was the heaviest and the LP line was the lightest, the differences between them

were also significant. Despite the significant differences and that these differences represent up to 15% of the averages of the trait; the values of the contrasts cannot be said to be economically relevant because the total dissectible fat represents a very low percentage of the carcass (Pla et al., 1996; Hernández et al., 2006). In our study, the contrasts for these traits between A and V lines are in agreement with studies by Hernández et al. (2006) and Zomeño et al. (2010) which showed that A line had more total dissectible fat than V line. In Gómez et al. (1998) no significant differences appeared for SFaW between A and V lines, but for PFaW, and as not observed in our experiment, the V line had more PFaW. It is necessary to take into account that Gómez et al. (1998) adjusted to a constant RCW. The reference carcass was dissected into four parts: hind leg, loin, fore leg and thoracic cage. The first three are preferred because of their meat content, package facility or cooking easiness, being consequently the most expensive cuts of the rabbit carcass (Montero, 2011). Generally, the line A was the heaviest for HLW, LW, FLW and TW closely followed by the LP, and then the V and H lines. Significant differences were found for HLW in the contrasts A-H, H-V and LP-H, for FLW in the contrast A-LP and for TW in the contrasts A-H, A-V, LP-H and LP-V.

Between the A and V lines, Gómez et al. (1998) showed that the A line was the lightest for FLW and non-significant differences for HLW, TW and LW were obtained. Hernández et al. (2006) studied differences between A and V lines in high priced cuts (loin and hind part) and these differences were very small. Brun (1993) showed that the increase of the litter size produces a reduction of the FLW. This is in disagreement with our results because we observed that the lines with heaviest FLW were A and LP lines. The A line came from litters with the lowest numbers of born alive (BA, 10.13) and the lowest number of weaned rabbit (NW, 8.76) but the LP line had the higher prolificacy

(12.30 BA and 10.56 NW). Despite some significant and relevant results in the retail cuts; at present, rabbit carcass prices are not established according to them. Perhaps, in the near future, it would be important take into account these traits to offer news products according to the new requirement of the consumers and packaging systems . The meat/bone ratio in the hind leg provides a good prediction for meatiness referred to RCW (Varewyck and Bouquet, 1982; Blasco et al., 1984; Hernández et al., 1996). The A line showed the highest value of M/B ratio and the V line had the lowest value for this trait, these results being significant. This finding is in agreement with Hernández et al. (2006) which showed that the A line had the largest M/B ratio. In our results it can observed that the association between CCW and RCW, and M/B ratio, resulted in higher values in the contrasts for carcass weights, which were also associated with high values for M/B ratio.

Table 3. Contrasts (standard error) between the lines for carcass quality traits.

Trait[1]	A-H	A-LP	A-V	H-V	LP-H	LP-V
CCW, g	83(38)*	22(27)	60(27)*	-22(26)	61(37)	38(27)
HW, g	9(3)*	3(2)	8(2)*	-1(2)	5(3)	4(2)*
LvW, g	-5(4)	1(3)	1(3)	7(3)*	-6(4)	1(3)
KiW, g	1(0.51)*	1(0.37)	1(0.37)*	0(0.35)	1(0.51)	0(0.36)
LHW, g	1(1.00)	-1(0.86)	0(0.85)	-1(0.82)	1(1.00)	0(0.85)
RCW, g	72(32)*	17(23)	49(23)*	-23(22)	55(32)	32(23)
SFaW, g	-1(0.65)	0(0.47)	0(0.46)	1(0.45)*	-1(0.64)	0(0.46)
PFaW, g	1(2)	3(1)*	1(1)	0(1)	-2(2)	-1(1)
HLW, g	36(11)*	0(8)	16(8)*	-20(8)*	36(11)*	15(8)
LW, g	14(12)	5(8)	15(8)	2(8)	8(12)	9(8)
FLW, g	9(6)	9(4)*	5(4)	-3(4)	0(6)	-3(4)
TW, g	14(5)*	0(3)	7(3)*	-7(3)*	14(5)*	8(3)*
M/B	0.30(0.22)	0.10(0.15)	0.36(0.15)*	0.06(0.15)	0.19(0.22)	0.25(0.15)

[1] . CW= commercial carcass weight, HW= head weight, LvW= liver weight, KiW= kidneys weight, LHW= thoracic viscera weight, RCW= reference carcasses weight, SFaW= scapular fat weight, PFaW= perirenal fat weight, HLW= hind leg weight, LW= loin weight, FLW= fore leg weight, TW= thoracic cage weight, M/B= meat to bone ratio, *$P < 0.05$ (significant difference at $\alpha = 0.05$).

On commercial farms, crossbred does are the most common type of females and, consequently, differences in slaughter and carcass traits due to dam effects are associated to the different types of crosses that might have importance. As mentioned in Chapter 2 for growth traits we considered these dam effects for the different crossbred groups (the average of a cross and its reciprocal) with respect to the V line (Tables 4 and 5). In an overall comparison of Tables 2 and 3 it was observed that the contrasts between crossbreds and line V were smaller than between pure lines, i.e. less significant differences were found for the crossbreds. For LW63 no significant differences were observed. In Chapter 2, we studied the same animals for body weight at 63 days and, also, did not observe significant differences, the small differences observed in both studies are probably that LW63 was measured after a day of fasting. For CSkW, FGTW and HCW, non-significant differences were observed, however, all crossbred groups shower higher CSkW than the V line. This is in agreement with the contrasts between lines (Table 2) that showed that the V line was the lightest for this trait. Regarding FGTW, in general, crossbreds involving A line were the heaviest and only the crossbred HV was lighter than the V line. This agrees with the result mentioned before that these lines (H and V) had the lightest gastrointestinal tracts. As pure lines, A and LP had the heaviest skin and full gastrointestinal tracts, and the crossbreds involving these lines showed the poorest DP (significant differences between AL-VV and LV-VV), although some of these differences reached an important magnitude, for example 0.8% for the contrast AL-VV, in favor of VV animals. For colour parameters, only significant differences appeared in the contrast AH-VV for a* and b*. This result agrees with the significant differences observed between A and V, and between H and V lines (Table 2) for the same traits. Non-significant differences were found for CCW; however, similar

Table 4. Contrasts (standard error) between crossbred genetic groups[1] and V line for slaughter and carcass colour traits**.**

Trait[2]	AH-VV	AL-VV	AV-VV	HV-VV	LH-VV	LV-VV	All-VV
LW63, g	13.93(37.50)	13.16(37.53)	-16.92(37.01)	-14.31(38.21)	12.67(36.90)	-1.58(37.03)	1.15(28.74)
CSkW, g	2.32(5.20)	9.96(5.20)	7.08(5.20)	4.65(5.34)	9.14(5.17)	8.11(5.18)	6.85(4.01)
FGTW, g	8.74(7.44)	12.68(7.43)	3.41(7.39)	-7.45(7.60)	2.44(7.35)	1.55(7.60)	3.55(5.70)
HCW, g	-0.14(24.00)	-9.65(24.00)	-21.31(23.80)	-7.28(24.40)	6.60(23.62)	-13.52(23.70)	-7.52(18.38)
DP, %	-0.44(0.31)	-0.82(0.30)*	-0.54(0.31)	0.07(0.31)	-0.11(0.31)	-0.62(0.30)*	-0.41(0.23)
L*	-0.13(0.31)	-0.54(0.31)	0.29(0.32)	-0.40(0.31)	-0.35(0.31)	-0.31(0.31)	-0.24(0.23)
a*	-0.44(0.13)*	-0.08(0.13)	-0.18(0.13)	-0.16(0.13)	-0.25(0.14)	-0.08(0.13)	-0.17(0.10)
b*	-0.56(0.24)*	-0.20(0.24)	-0.18(0.24)	-0.07(0.24)	-0.20(0.24)	-0.20(0.24)	-0.21(0.18)

[1] . One cross and its reciprocal are considered together. [2] . LW63= liveweight at 63 days after fasting, CSkW= commercial skin weight, FGTW= full gastrointestinal tract weight, HCW= hot carcass weight, DP= dressing percentage, L*= lightness of loin surface, a*= redness of loin surface, b*= yellowness of loin surface. *$P < 0.05$ (significant difference at $\alpha = 0.05$). L=LP line.

to result involving line comparisons (Table 3) regarding the association between HCW and CCW whereby a negative association was observed. The explanation could be the same due to the sampling effect in the line comparison.

No significant differences were obtained for HW, LvW and KiW. In this case the magnitudes of the contrasts were small.

For LHW, significant differences were observed between AH and VV, LH and VV, LV and VV and All and VV. Despite these differences, they represent in some cases up to 8% of the averages of the trait; however, the values of the contrasts cannot be said to be economically relevant. Non-significant differences were obtained for RCW. For dissectible fat a significant difference between AL and VV regarding PfaW was observed. However, the magnitude of the contrast was low. The rest of the contrasts regarding dissectible fat were all not significant. For the principal carcass cut traits, only the contrast LH-VV for LW showed a significant effect in favor of the LH, and for the same contrast HLW was close to significance. These differences, around 3% the mean of the traits, may be important, because loin and hind legs are very important economical cuts of the carcass and are usually important meat quality traits as varying levels of proteins, lipids, tenderness, flavour, etc., are measured in them (Pla et al., 1996; Hernandez et al., 2006). For M/B ratio, line V was superior to all crossbred genetics groups (being significant for HV-VV and All-VV). This is in disagreement with results obtained in the lines comparisons (Table 3) where line V had the lowest M/B ratio.

Table 5. Contrasts (standard error) between crossbred genetic groups[1] and V line for carcass quality traits**.**

Trait[2]	AH-VV	AL-VV	AV-VV	HV-VV	LH-VV	LV-VV	All-VV
CCW, g	8.06(19.47)	-18.30(19.32)	6.91(19.46)	-15.08(19.34)	31.46(19.37)	-17.91(19.32)	-0.80(14.67)
HW, g	0.87(1.53)	0.12(1.52)	-0.03(1.53)	0.17(1.53)	2.63(1.53)	-1.42(1.53)	0.39(1.16)
LvW, g	0.87(2.13)	-2.53(2.12)	1.02(2.15)	-3.59(2.14)	3.24(2.13)	1.36(2.13)	0.06(1.62)
KiW, g	-0.19(0.26)	-0.43(0.26)	-0.05(0.26)	-0.07(0.26)	0.21(0.0.26)	-0.07(0.26)	-0.10(0.20)
LHW, g	-2.16(0.61)*	-0.39(0.60)	0.22(0.61)	-0.84(0.60)	-2.01(0.60)*	-2.01(0.60)*	-1.19(0.46)*
RCW, g	11.07(16.60)	-11.56(16.52)	6.60(16.64)	-10.51(16.59)	26.99(16.60)	-16.63(16.56)	0.99(12.56)
SFaW, g	-0.36(0.33)	-0.30(0.34)	-0.20(0.33)	-0.03(0.33)	-0.24(0.34)	-0.15(0.34)	-0.03(0.25)
PFaW, g	0.98(0.96)	-2.06(0.95)*	0.01(0.96)	-0.67(0.96)	1.55(0.96)	0.21(0.96)	0.00(0.73)
HLW, g	-1.06(5.87)	-0.80(5.84)	1.49(5.88)	-6.90(5.86)	10.22(5.88)	-6.36(5.85)	-0.57(4.44)
LW, g	8.82 (6.16)	-4.12(6.16)	6.50(6.17)	1.24(6.15)	12.40(6.16)*	-2.13(6.15)	3.77(4.66)
FLW, g	-2.82(3.16)	5.04(3.15)	-1.91(3.17)	-0.72(3.16)	5.15(3.16)	-2.48(3.16)	-1.30(2.40)
TW, g	0.50(2.56)	-2.48(2.54)	2.91(2.56)	-2.15(2.56)	0.71(2.56)	-3.51(2.55)	-0.67(1.94)
M/B	-0.09(0.11)	-0.07(0.11)	-0.17(0.11)	-0.25(0.11)*	-0.23(0.11)	-0.21(0.11)	-0.17(0.08)*

[1] . One cross and its reciprocal are considered together.[2] . CW= commercial carcass weight, HW= head weight, LvW= liver weight, KiW= kidneys weight, LHW= thoracic viscera weight, RCW= reference carcasses weight, SFaW= scapular fat weight, PFaW= perirenal fat weight, HLW= hind leg weight, LW= loin weight, FLW= fore leg weight, TW= thoracic cage weight, M/B= meat to bone ratio, L=LP line *$P < 0.05$ (significant difference at $\alpha = 0.05$).

The importance of using a particular line either as sire or dam in a cross was assessed by testing the differences between a particular cross and its reciprocal (Tables 6 and 7). Because a given cross and its reciprocal were raised on different farms, but connected by the line V that was raised on all the farms, the consequence of this is that the standard errors of the contrasts for the reciprocal effect (Tables 6 and 7) were higher than for the contrasts between the lines raised on the same farm (Tables 2 and 3) and for the average of a cross and its reciprocal with respect to line V (Tables 4 and 5). The contrasts for the traits that were measured in the slaughterhouse were not significant. Given the large errors obtained for these contrasts, this means that relevant differences might exist between reciprocal crosses but they could not be statistically detected. This could be important in LW63 and DP because these traits are the most economically relevant. For traits measured in the meat laboratory, significant differences for the contrast AV-VA were observed for a*, CCW, LHW, RCW, SFaW, PFaW, HLW, LW and FLW. Clearly, for this cross the best performance were obtained when the A line served as the sire. Only for SFaW and PFaW was this contrast considered to be economically unfavorable, but since the commercial rabbit carcass is quite lean, this is not a problem at all. For the rest of the contrasts between the reciprocal crosses, the situation was not clear as to whether a cross is preferable over its reciprocal. In Chapter 2, we studied the same reciprocal crosses for body weight at 63 days, and, in agreement with our results, they did not observe any significant differences. Ragab (2012) studied the same crosses for reproductive traits and observed non-significant differences between reciprocal crosses for the number born alive and weaned. In Chapter 2, we showed significant differences between reciprocal crosses in feed conversion ratio in the contrasts AH-HA and LH-HL (the H line was better as dam).

Table 6. Contrasts (standard error) between reciprocal crosses for slaughter and carcass colour traits.

Trait[1]	AH-HA	AL-LA	AV-VA	HV-VH	LH-HL	LV-VL
LW63, g	13(75)	-37(75)	46(74)	49(76)	-46(75)	-47(74)
CSkW, g	3(10)	-9(10)	-1(10)	9(10)	-4(10)	-2(10)
FGTW, g	2(15)	-6(15)	-13(15)	8(15)	-4(15)	-16(15)
HCW, g	24(48)	-32(48)	43(48)	34(47)	-32(47)	-36(47)
DP, %	0.62(0.61)	-0.30(0.61)	0.76(0.61)	0.32(0.63)	-0.30(0.61)	-0.26(0.61)
L*	0.90(0.62)	-0.13(0.62)	-0.05(0.63)	1.00(0.62)	0.16(0.63)	0.94(0.62)
a*	-0.60(0.25)*	0.40(0.25)	0.51(0.25)*	-0.17(0.25)	0.31(0.25)	0.11(0.25)
b*	-0.30(0.46)	0.40(0.46)	0.40(0.46)	0.70(0.46)	0.48(0.46)	0.14(0.46)

[1] . LW63= liveweight at 63 days after fasting, CSkW= commercial skin weight, FGTW= full gastrointestinal tract weight, HCW= hot carcass weight, DP= dressing percentage, L*= lightness of loin surface, a*= redness of loin surface, b*= yellowness of loin surface. *$P < 0.05$ (significant difference at $\alpha = 0.05$). L=LP line. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 7. Contrasts (standard error) between reciprocal crosses for carcass quality traits.

Trait[1]	AH-HA	AL-LA	AV-VA	HV-VH	LH-HL	LV-VL
CCW, g	71(37)	-15(37)	99(37)*	56(37)	32(37)	-35(37)
HW, g	-7(3)*	-3(3)	4(3)	7(3)*	4(3)	-6(3)*
LvW, g	7(4)	1(4)	6(4)	4(4)	-3(4)	0(4)
KiW, g	1(0.5)	0(0.5)	1(0.5)	1(0.5)	0(0.5)	0(0.5)
LHW, g	0(1)	0(1)	3(1)*	2(1)	0(1)	0(1)
RCW, g	54(32)	-15(32)	85(32)*	45(32)	30(32)	-29(32)
SFaW, g	1(1)	1(1)	2(1)*	0(1)	0(1)	0(1)
PFaW, g	1(2)	2(2)	5(2)*	2(2)	0(2)	1(2)
HLW, g	15(11)	-2(11)	26(11)*	14(11)	8(11)	-4(11)
LW, g	13(11)	-3(11)	27(11)*	17(11)	13(11)	-20(11)
FLW, g	13(6)*	-5(6)	12(6)*	14(6)*	11(6)	-4(6)
TW, g	7(5)	-4(5)	5(5)	5(5)	5(5)	-5(5)
M/B	-0.27(0.22)	0.26(0.22)	0.29(0.22)	-0.15(0.22)	0.08(0.22)	0.43(0.22)

[1] CW= commercial carcass weight, HW= head weight, LvW= liver weight, KiW= kidneys weight, LHW= thoracic viscera weight, RCW= reference carcasses weight, SFaW= scapular fat weight, PFaW= perirenal fat weight, HLW= hind leg weight, LW= loin weight, FLW= fore leg weight, TW= thoracic cage weight, M/B= meat to bone ratio, L=LP line *$P < 0.05$ (significant difference at $\alpha = 0.05$).

The information on reciprocal crosses regarding reproduction, growth, carcass and slaughter traits must be integrated by the technician in order to decide the best line to act as dam or as sire, according to the objectives of the farm.

5.4.3 Direct-maternal effects.

Differences between direct-maternal effects are shown in Tables 8 and 9. The results of the contrasts between lines (Tables 2 and 3) are in close agreement with the results for direct-maternal differences between lines. However, it can be observed that the standard errors in Tables 8 and 9 are greater than those for the corresponding contrasts in Tables 2 and 3, showing that our experiment had higher power in detecting differences between lines, than differences between direct-maternal effects. For LW63, there were no significant differences, but there were some indications that the direct-maternal effects of the LP line were the highest. This result partially agrees with results by Mínguez et al. (2012), where the LP line was found to be heavier than A and V lines, but not heavier than the H line. Orengo et al. (2009) studied crossbreeding parameters for growth traits between A and V lines, like us, however they did not find any relevant difference for body weight at 60 days between these lines for direct genetics effects. For CSkW, the V line had the lowest effect; correspondingly the contrasts A-V and L-V in Table 2 followed the same pattern. Regarding FGTW and HCW, no significant differences were found. Regarding LW63, CSkW, FGTW, HCW and DP, it was observed the same pattern as for the differences between the lines. When the contrast in CSkW and FGTW had the same sign, positive in both cases, significant negative differences in DP were observed. This is because in these cases the differences between LW63 and HCW became high. G^{I}_{A-H}, G^{I}_{L-H} and G^{I}_{L-V} **,** reaching significant values for DP, in favor of the line H in A-H and L-H, and in favor of the L line in L-V, as occurred

for the contrasts between the lines (Table 2). In Table 2, the contrast A-V was significant, but this does not appear in Table 8 for the corresponding contrast; however, G^I_{A-V} was close to be significant. The magnitude of these differences and the importance of this trait indicate a relevant influence due to these direct-maternal differences, including the possible differences that in Table 8 were not significant. In the colour parameters of the carcass, there were no significant differences for L*, but significant estimates appeared for a* for G^I_{A-V}, G^I_{H-V} and G^I_{L-V}, ; in these cases the line V had the highest values. Non-significant differences were found for the contrasts in b*. Thus, the concordance for the significant differences between the Tables 2 and 3 and the Tables 8 and 9 is not complete because of the grand-maternal effects and the error of the models. Line A had the highest effect on CCW and HW with significant differences were detected between this line and the others. For these traits, there were also significant values for G^I_{L-V} in favor of the L line. The corresponding significant contrast involving line L for CCW and HW did not reach significance in Table 3, but they were in the same direction. Given the magnitude of the contrasts for CCW, up to 11% the mean of the trait, and the economic importance of the trait it makes these direct-maternal differences relevant. There were significant estimates in LvW for G^I_{A-L}, G^I_{A-V} and G^I_{H-V}, in favor of the lines A and H, but which did not have the same corresponding significant results in the contrasts between the lines (Tables 2 and 3). For KiW, G^I_{A-V} was significant in the contrast A-V found in Table 3. However, there were significant differences between the A and H lines (contrast A-H, in favor of the A line), but not significant differences between the direct-maternal effects of these lines. Non-significant differences were observed for LHW. Table 9 shows, for RCW, significant estimates of G^I_{A-H}, G^I_{A-V} and G^I_{L-V} that were in favor of the A and LP lines. The effects

on these traits had a high relationship with the effects on CCW, as also observed in Table 3.

The direct-maternal differences for the fat weights (SFaW and PFaW) were significant between the lines A and LP and between the lines A and V, but they were not economically relevant. HLW is an important cut in the carcass rabbit and G^I_{A-H}, G^I_{A-V}, G^I_{L-H} and G^I_{L-V} were significant in favor of the A and LP lines. For LW, a significant estimate was found for G^I_{A-V}; in addition, G^I_{A-H} and G^I_{A-L} effects were close to being significant. For FLW, the A line showed the largest effects with significant estimates of G^I_{A-H}, G^I_{A-L} and G^I_{A-V}. As for HLW, significant estimates were found for TW in G^I_{A-H}, G^I_{A-V}, G^I_{L-H} and G^I_{L-V}, results that agree with the corresponding contrasts between lines found in Table 3. Significant differences for M/B ratio were found in G^I_{A-V} and G^I_{L-V}.

Piles et al. (2004) obtained significant direct genetic effects for live weight at 60 d in a crossbreeding experiment using animals from C and R lines. Similarly, Ouyed et al. (2008) obtained significant direct effects for LW63 and DP between Californian (CA) and New-Zealand White (NZ) breeds. Al-Saef et al. (2009), using crosses between the V line and the Saudi Gabali, found that, in general, the effects of the V line were higher than the effects of the Saudi Gabali. These effects were significant for live weight, HCW, DP, HW and LHW, but the fattening period finished much later at 84 days of age.

Table 8. Direct-maternal differences between lines[1] (standard error) for slaughter and carcass colour traits.

Trait[2]	[1] G^I_{A-H}	G^I_{A-L}	G^I_{A-V}	G^I_{H-V}	G^I_{L-H}	G^I_{L-V}
LW63, g	13(85)	-10(67)	81(67)	68(67)	23(86)	91(67)
CSkW, g	6(12)	3(9)	25(10)*	19(9)*	2(12)	21(9)*
FGTW, g	8(17)	-5(13)	4(13)	-4(13)	13(17)	9(13)
HCW, g	-27(54)	8(43)	22(43)	49(43)	-35(55)	13(43)
DP, %	-1.44(0.68)*	0.63(0.53)	-0.93(0.53)	0.51(0.53)	-2.13(0.68)*	-1.61(0.53)*
L*	0.11(0.67)	-0.34(0.56)	0.53(0.54)	0.42(0.54)	0.50(0.65)	0.91(0.51)
a*	0.01(0.29)	0.05(0.23)	-0.46(0.23)*	-0.46(0.23)*	-0.05(0.29)	-0.52(0.23)*
b*	-0.07(0.54)	-0.15(0.42)	-0.60(0.42)	-0.52(0.42)	0.07(0.54)	-0.45(0.42)

[1]. G^I_{i-j} , direct-maternal differences between lines i and j (see text for a complete explanation), [2] . LW63= liveweight at 63 days after fasting, CSkW= commercial skin weight, FGTW= full gastrointestinal tract weight, HCW= hot carcass weight, DP= dressing percentage, L*= lightness of loin surface, a*= redness of loin surface, b*= yellowness of loin surface. *$P < 0.05$ (significant difference at $\alpha = 0.05$). L=LP line. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 9. Direct-maternal differences between lines[1] (standard error) for carcass quality traits.

Trait[2]	[1] G^I_{A-H}	G^I_{A-L}	G^I_{A-V}	G^I_{H-V}	G^I_{L-H}	G^I_{L-V}
CCW, g	133(43)*	71(34)*	142(34)*	9(33)	63(43)	71(34)*
HW, g	12(3)*	7(3)*	13(3)*	1(3)	5(3)	61(3)*
LvW, g	-2(5)	6(4)*	9(4)*	11(4)*	-8(5)	3(4)
KiW, g	1(0.6)	0(0.4)	2(0.4)*	1(0.4)	1(0.6)	1(0.4)
LHW, g	1(1)	0(1)	2(1)	1(1)	1(1)	2(1)
RCW, g	114(37)*	55(29)	116(29)*	2(29)	59(37)	61(29)*
SFaW, g	0(0.7)	1(0.5)*	2(0.5)*	1(0.5)	-1(0.7)	0(0.5)
PFaW, g	3(2)	5(2)*	6(2)*	2(2)	-2(2)	0(2)
HLW, g	48(13)*	11(10)	37(10)*	-11(10)	37(13)*	26(10)*
LW, g	26(14)	20(11)	35(11)*	9(11)	5(14)	15(11)
FLW, g	17(7)*	14(6)*	19(5)*	3(5)	2(7)	5(5)
TW, g	18(6)*	2(4)	13(4)*	-5(4)	15(6)*	10(4)*
M/B	0.35(0.25)	0.02(0.20)	0.47(0.20)*	0.11(0.20)	0.34(0.25)	0.45(0.20)*

[1]. G^I_{i-j} , direct-maternal differences between lines i and j (see text for a complete explanation,[2] . CW= commercial carcass weight, HW= head weight, LvW= liver weight, KiW= kidneys weight, LHW= thoracic viscera weight, RCW= reference carcasses weight, SFaW= scapular fat weight, PFaW= perirenal fat weight, HLW= hind leg weight, LW= loin weight, FLW= fore leg weight, TW= thoracic cage weight, M/B= meat to bone ratio, L=LP line *$P < 0.05$ (significant difference at $\alpha = 0.05$).

5.4.4 Grand-maternal effects.

Grand-maternal effect differences between lines are shown in Tables 10 and 11. Comparing the standard errors of the corresponding contrasts for direct-maternal effects (Tables 8 and 9) and grand-maternal effects (Table 10 and 11), it can be observed that the errors for the latter are smaller than those for the former, showing that our data structure is better suited to estimate grand-maternal effects than direct-maternal effects, the same result was observed in Chapter 2. However, the number of contrasts found to be significant for grand-maternal effects are fewer than for direct-maternal effects, clearly indicating that direct-maternal effects are more important than grand-maternal effects. For slaughter traits, non-significant estimates were found, with the only exception of $G^{M'}_{L-V}$ for CSkW, which was significant in favor of V line. In Chapter 2, we found a significant estimate for $G^{M'}_{L-V}$ in body weight at 63 days for the same sample but only before fasting. For colour traits, there were significant estimates in L* for $G^{M'}_{A-H}$, in a* for $G^{M'}_{A-H}$, $G^{M'}_{A-L}$ and $G^{M'}_{A-V}$ and in b* for $G^{M'}_{A-V}$, all these contrasts favored the A line.

Table 11 shows significant estimates in $G^{M'}_{A-H}$, $G^{M'}_{A-L}$ and $G^{M'}_{A-V}$ for CCW, favoring the lines other than A. These contrasts were also significant for the direct-maternal effects (Table 9). However, in the case of the grand-maternal differences between lines, the values of the contrasts were smaller and of opposite sign. Moreover, the contrast for CCW in Table 11 did not show any similarity with the corresponding contrasts of reciprocal effects (Table 7).

For HW, line A had the smallest effect while V line had the largest effect. No significant differences were found for LvW, and the significant differences detected for KiW ($G^{M'}_{A-V}$) and for LHW ($G^{M'}_{L-V}$) had a low magnitude. For RCW, as for CCW, A line

showed the highest value, but again, these results do not match those found in Table 5, being the opposite to the contrasts regarding direct-maternal effects (Table 9). For dissectible fat weights, significant differences were not observed. With regards to carcass cuts, it was observed that grand-maternal effects associated to A line were unfavorable. The V line showed the most favorable grand-maternal effects for M/B - for this trait the contrast $G_{L-V}^{M'}$ was not significant but the magnitude of the difference was high. Afifi et al. (1994), Piles et al. (2004), Ouyed et al. (2008) and Al-Saef et al. (2009) reported that these effects were not significant for the traits measured in our study.

Table 10. [1]Grand-maternal differences between lines (standard error) for slaughter and carcass colour traits.

Trait[2]	[1] $G_{A-H}^{M'}$	$G_{A-L}^{M'}$	$G_{A-V}^{M'}$	$G_{H-V}^{M'}$	$G_{L-H}^{M'}$	$G_{L-V}^{M'}$
LW63, g	-12(46)	-34(53)	-59(61)	-47(46)	22(45)	-25(54)
CSkW, g	-6(6)	4(7)	-11(8)	-4(6)	-11(6)	-16(7)*
FGTW, g	0(9)	-8(10)	-1(12)	2(9)	8(9)	6(10)
HCW, g	8(29)	-6(34)	-12(39)	-21(29)	14(29)	-7(34)
DP, %	0.59(0.37)	0.59(0.42)	0.78(0.49)	0.19(0.37)	0.01(0.37)	0.20(0.43)
L*	-0.90(0.38)*	-0.56(0.42)	-0.48(0.46)	0.41(0.38)	-0.33(0.38)	0.07(0.43)
a*	0.43(0.16)*	0.42(0.18)*	0.51(0.20)*	0.08(0.16)	0.00(0.16)	0.08(0.18)
b*	0.40(0.30)	0.27(0.34)	0.75(0.38)*	0.35(0.30)	0.13(0.30)	0.48(0.35)

[1]. $G_{i-j}^{M'}$ **,** grand-maternal differences between lines i and j (see text for a more complete explanation), [2]. LW63= liveweight at 63 days after fasting, CSkW= commercial skin weight, FGTW= full gastrointestinal tract weight, HCW= hot carcass weight, DP= dressing percentage, L*= lightness of loin surface, a*= redness of loin surface, b*= yellowness of loin surface. *$P < 0.05$ (significant difference at $\alpha = 0.05$). L=LP line. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 11. [1]Grand-maternal differences between lines (standard error) for slaughter and carcass quality traits.

Trait[2]	[1] $G_{A-H}^{M'}$	$G_{A-L}^{M'}$	$G_{A-V}^{M'}$	$G_{H-V}^{M'}$	$G_{L-H}^{M'}$	$G_{L-V}^{M'}$
CCW, g	-45(23)*	-57(27)*	-69(30)*	-23(23)	12(23)	-11(27)
HW, g	-2(2)	-3(2)	-6(2)*	-4(2)*	1(2)	-2(2)
LvW, g	-4(3)	0(3)	-4(3)	0(3)	-4(3)	-4(3)
KiW, g	-1(0.3)	-1(0.4)	-1(0.4)*	0(0.3)	0(0.3)	0(0.4)
LHW, g	-1(1)	1(1)	-1(1)	0(1)	-2(1)	-2(1)*
RCW, g	-35(20)	-51(23)*	-53(26)*	-18(20)	16(20)	-2(23)
SFaW, g	-0.5(0.4)	0(0.4)	-0.5(0.5)	0(0.4)	-0.5(0.4)	-0.5(0.4)
PFaW, g	-1(1)	-2(1)	-2(2)	-1(1)	1(1)	0(1)
HLW, g	-10(7)	-17(8)*	-16(9)	-6(7)	7(7)	1(8)
LW, g	-15(7)*	-17(8)*	-16(10)	-1(8)	2(6)	1(9)
FLW, g	-2(4)	-2(4)	-6(5)	-5(4)	-1(4)	-4(4)
TW, g	-10(3)*	-10(4)*	-10(4)*	-1(3)	1(3)	0(4)
M/B	-0.02(0.13)	-0.07(0.15)	-0.35(0.17)*	-0.36(0.13)*	0.06(0.13)	-0.30(0.16)

[1]. $G_{i-j}^{M'}$ **,** grand-maternal differences between lines i and j (see text for a more complete explanation). [2] . CW= commercial carcass weight, HW= head weight, LvW= liver weight, KiW= kidneys weight, LHW= thoracic viscera weight, RCW= reference carcasses weight, SFaW= scapular fat weight, PFaW= perirenal fat weight, HLW= hind leg weight, LW= loin weight, FLW= fore leg weight, TW= thoracic cage weight, M/B= meat to bone ratio, L=LP line *$P < 0.05$ (significant difference at $\alpha = 0.05$).

5.4.5 Maternal heterosis.

Estimates of maternal heterosis effects are shown in Tables 12 and 13. A result which clearly draws attention is that the sign of the majority of the estimates for slaughter and carcass traits were negative. Many results of positive heterosis for litter size have been reported (Brun and Saleil, 1994; Khalil and Afifi, 2000; Baselga, et al. 2003; Brun and Baselga, 2005; Youssef et al., 2008; Ragab, 2012). In larger sized litters involving crossbred versus purebred does, this would penalize body weights (Rouvier et al., 1973; Johnson et al., 1988; Lukefahr et al., 1990; Ferguson et al., 1997). This influence would involve the contrasts between lines where the relationships between LW63 and slaughter traits and between CCW and carcass traits were observed. Notice that the estimates involved the lines with higher prolificacy (H and LP lines) (Ragab, 2012), showing significant and negative values for their corresponding estimates of maternal heterosis, H_{LH}^{M}, which appeared for the majority of the traits measured in the laboratory. However, these significant heterosis values only seem relevant for CCW, RCW and cut parts between the lines LP and H, for HLW and M/B between the lines A and H and for M/B between the lines A and LP; in all these cases differences of up to 5% of the mean were observed. The design of the experiment did not allow for the estimation of the direct heterosis effect, but this effect is expected to be small (Orengo et al., 2009). The maternal heterosis effects obtained in this study could be related to the effects through prolificacy on growth. However, if the estimates of the maternal heterosis are done including the number born alive as a covariate in the analysis of the traits the results are very similar. Actually, the only significant regression coefficients were for CSkW (-1.45±0.26 g/rabbit), FGTW (-3.06±1.20 g/rabbit) and HCW (-13.44±1.17 g/rabbit). The results obtained in other experiments are highly variable and have not been related to litter size of the dams. Thus, Piles et al. (2004) did not obtain

significant differences for heterosis in a crossbreeding experiment using animals from C and R strains. With Californian, American Chinchilla and New-Zealand White breeds, Ouyed et al. (2011) generally obtained zero or low heterosis for body conformation and carcass traits. Al-Saef et al. (2009), using crosses between the V line and the Saudi Gabali, obtained heterosis estimates that were mostly positive, but significance was observed for only CSkW, HW and LHW. Significant and negative values of heterosis were found by Zabadilová et al. (2008) in different crosses between two HYPLUS lines for live weight, carcass weight and hind leg weight. However, it should be noted that in Al-Saef et al. (2009) and Zabadilová et al. (2008), the young rabbits were slaughtered at 84 days of age.

Table 12. [1]Maternal heterosis (standard error) for slaughter and carcass colour traits.

Trait[2]	[1] H_{AH}^{M}	H_{AL}^{M}	H_{AV}^{M}	H_{HV}^{M}	H_{LH}^{M}	H_{LV}^{M}
LW63, g	-46(46)	-47(53)	-26(46)	-43(40)	-27(38)	2(36)
CSkW, g	-2(6)	-7(7)	-2(6)	-6(5)	-1(5)	-2(5)
FGTW, g	-7(9)	-4(10)	-5(9)	0(8)	6(8)	9(8)
HCW, g	-18(30)	-10(34)	-16(30)	-30(25)	-28(25)	0(23)
DP, %	0.26(0.37)	0.65(0.43)	-0.04(0.37)	-0.29(0.33)	-0.56(0.32)	-0.14(0.30)
L*	-0.37(0.37)	-0.32(0.43)	-0.31(0.38)	-0.60(0.33)	-0.79(0.33)*	-079(0.31)*
a*	0.41(0.16)*	0.33(0.18)	0.09(0.16)	-0.04(0.13)	-0.07(0.13)	-0.14(0.13)
b*	0.21(0.30)	0.72(0.34)	0.58(0.29)*	-0.48(0.25)	-0.48(0.25)	-0.37(0.25)

[1]. H_{ij}^{M} maternal heterosis between lines i and j, [2]. LW63= liveweight at 63 days after fasting, CSkW= commercial skin weight, FGTW= full gastrointestinal tract weight, HCW= hot carcass weight, DP= dressing percentage, L*= lightness of loin surface, a*= redness of loin surface, b*= yellowness of loin surface. *P < 0.05 (significant difference at α = 0.05). L=LP line. *P < 0.05 (significant difference at α = 0.05).

Table 13. [1]Maternal heterosis (standard error) for carcass quality traits.

Trait[2]	[1] H_{AH}^{M}	H_{AL}^{M}	H_{AV}^{M}	H_{HV}^{M}	H_{LH}^{M}	H_{LV}^{M}
CCW, g	-36(23)	23(27)	-3(23)	-31(20)	-81(20)*	-32(19)
HW, g	-3(2)	-1(2)	-1(2)	2(2)	-5(2)*	-1(2)
LvW, g	1(3)	-1(3)	-7(3)*	-3(2)	-7(2)*	-2(2)
KiW, g	0(0.3)	0(0.4)	0(0.3)	-1(0.3)*	-1(0.3)*	0(0.3)
LHW, g	-2(0.7)*	-2(0.8)*	0(0.7)	-2(0.6)*	-2(0.6)*	-1(0.6)
RCW, g	-32(20)	22(23)	1(20)	-25(17)	-66(17)*	-29(17)
SFaW, g	0(0.4)	-1(0.4)*	-1(0.4)	0(0.3)	-1(0.3)*	0(0.3)
PFaW, g	1(1)	2(1)	-1(1)	-2(1)*	-4(1)*	-2(1)
HLW, g	-14(7)*	12(8)	3(7)	-9(6)	-21(6)*	-10(5)
LW, g	-7(7)	7(8)	0(7)	-8(6)	-19(6)*	-5(6)
FLW, g	-1(4)	8(4)	1(4)	-6(3)	-13(3)*	-8(3)*
TW, g	-8(3)	0(3)	1(3)	-1(3)	-4(3)	-2(3)
M/B	-0.39(0.13)*	-0.34(0.15)*	-0.25(0.13)	-0.06(0.11)	-0.11(0.11)	-0.20(0.11)

[1]. H_{ij}^{M} maternal heterosis between lines i and j, [2]. CW= commercial carcass weight, HW= head weight, LvW= liver weight, KiW= kidneys weight, LHW= thoracic viscera weight, RCW= reference carcasses weight, SFaW= scapular fat weight, PFaW= perirenal fat weight, HLW= hind leg weight, LW= loin weight, FLW= fore leg weight, TW= thoracic cage weight, M/B= meat to bone ratio, L=LP line *$P < 0.05$ (significant difference at $\alpha = 0.05$).

5.5 CONCLUSIONS.

Few significant differences were found between lines, but these differences seem to be relevant for DP and CCW. Results showed that the A line was the best for DP and for the heaviest CCW, while V line showed the poorest DP and the lightest CCW. Regarding the comparisons between the crosses and V line, the pure line V was only superior for the differences involving M/B ratio. In general, the reciprocal cross effects were not relevant, but only for the cross AV. It was observed that for carcass traits the performance of the cross was better when the line A served as the sire. 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 effects to those obtained in the comparison between lines and crosses were obtained for the direct-maternal effects. However, grand-maternal effects, in general, were of lower magnitude and of opposite sign than direct-maternal effects; also negative values of maternal heterosis were observed.This result could be explained, although it was not tested, by the negative environmental effect that crossbred females provide to their offspring as a consequence of their larger litter sizes compared to the purebred females. However, despite this relationship between growth and litter traits, it has not been common to find negative maternal heterosis in growth traits.

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CHAPTER 6

Genetic analysis of meat quality traits in the progeny of rabbit does from a diallel cross.

6.1 ABSTRACT

Young rabbits were from dams that were produced from a full diallel cross among four maternal lines and the sires from a single paternal line that produced sixteen genetic groups. A study was carried out to evaluate the genetic groups and to estimate the crossbreeding genetic parameters of meat quality traits measured in the *Longissimus* muscle (LM). The maternal lines (A, V, H and LP) were selected for litter size at weaning and the paternal line (R) was selected for postweaning average daily gain. The pH was measured in 950 LM. The remaining meat quality traits were recorded by NIRS from a sample of 285 LM that were used previously to measure pH. The sixteen genetic groups were distributed on four Spanish farms but only one genetic group (V) was present on all farms in order to connect records among these farms and to be used as reference group. Crossbreeding parameters were estimated according to Dickerson's model.

For pH, the A line had a significant difference with LP line of 0.05, although this difference was not relevant. No differences in protein were found. The line A had significant differences with V line for intramuscular fat, and fatty acids groups (SFA, MUFA, PUFA, n-3PUFA and n-6PUFA) of 0.23, 67, 66, 34 3.1 and 25 (mg/100 g of muscle), respectively. No significant differences appeared for the rest of lines, but it seemed that the line A had the higher values for these traits. Significant differences for these traits appeared between the crossbred AH and VV (in favor of AH) of 0.15, 47, 40, 20, 2.1 and 19 (mg/100 g of muscle), respectively. No significant differences were

found for meat quality traits for the rest of the contrasts. Significant differences were found in the contrast HV-VH for L* and a* in favor of the line V as sire. For the contrast AV-VA, the significant difference in SFA was in favor of A as sire (70 mg/100g muscle) because this crossbred (AV) had the smaller value, which was one of the main aims to reduce the SFA.

In estimation of crossbreeding parameters, grandmaternal and maternal heterosis effects were not significant. Between A and LP lines there were significant differences in direct-maternal effects for pH (0.08) and between A and V for intramuscular fat, and fatty acids groups (SFA, MUFA, PUFA, n-3PUFA and n-6PUFA) of 0.20, 63, 61, 33 and 2.9, respectively, in favor of the A line.

Keywords: crossbreeding parameters, diallel cross, meat quality traits, maternal lines, rabbits.

6.2 INTRODUCTION.

Meat rabbit selection programmes aims to improve, among other traits, litter size in dam lines and growth rate in sire lines (Rochambeau 1988; Baselga 2004). Maximizing growth potential of sire lines is important to ensure the economic viability of rabbits producers (Cartuche et al., 2013); however, it can produce an undesirable effect on meat and carcass qualities because the degree of maturity at market weight is reduced (Pascual, 2007). Meat quality is a generic term used to describe properties and perceptions of meat: sensory characteristics, nutritional properties, healthiness, technological factors, microbiological and chemical safety and ethical and environment aspects. Rabbit meat has good nutritive properties because it has lower fat and higher polyunsaturated fatty acid (**PUFA**) content than other meats (Hernández and Gondret, 2006). The most ubiquitous fatty acids (**FA**) are palmitic (C16:0), oleic (C18:1 n-9) and linoleic (C18:2 n-6) acids with percentages higher than 20% of total FA. Rabbit meat

also contains high protein content and high levels of essential amino acids (Hernández and Dalle Zote, 2010).

Conventional methods used to determine meat chemical composition are laborious, expensive, time-consuming and even destructive. New methods for meat quality evaluation have been used by researchers, as e.g. ultrasound, electric nose, tastes sensing, NIRS, TOBEC and Video Image Analysis (Cross and Belk, 1992). NIRS (near infrared reflectance spectroscopy) is a fast, accurate and inexpensive analytical technique and rabbit is a good experimental model to measure meat quality.

The objective of this work was to estimate line differences and crossbreeding parameters (the dams of which come from a full diallel-cross among four maternal lines and the sires from a paternal line) for certain traits relating to meat chemical composition based on NIRS measurements in rabbits to evaluate the impact of a large genetic improvement program in meat rabbits on meat quality.

6.3 MATERIAL AND METHODS.

6.3.1 Animals.

The present study involved animals whose dams came from a full diallel cross among four maternal lines (A, V, H and LP) and their sires from a single paternal line (R). Thus, the maternal genetic groups involved in the experiment represented four 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. L is used to identify the LP line as sire or dam of a genetic group. The animals used for this study were the same rabbits used in Chapter 3 to measure carcass traits.

6.3.2 Crossbreeding Design and Management.

The study was carried out on four different farms, located in Altura (Castellón, Spain), Rioseco de Tapia (León, Spain), Valencia (Spain) and Sant Carles de la Rápita (Tarragona, Spain). On each farm, the same experimental design was performed. The distribution of the does on the farms is shown in Chapter 2. The genetic group VV was present on all farms allowing for data connections across farms, but because this was the only genetic type on all the farms no interaction between farm and genetic type could be considered.

Twenty-five females of 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. Placing animals in the same cage that belonged to the same litter was avoided, but they always belonged to the same genetic group. During post-weaning period, rabbits were fed *ad libitum* a standard commercial pellet diet and fresh water.

The whole fattening period lasted for five weeks on all the farms. On the farm of Altura data collection took place from February 1st 2011 to March 8th 2011; in Rioseco de Tapia from May 9th 2011 to June 13th 2011; in UPV from February 21st 2012 to March 27th 2012, and in San Carlos de la Rápita 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 mortality was unequal across genetic groups, thus the distribution of animals by genetic group was unbalanced. The observed mortality could be consequence of the intense weekly manipulations of young rabbits for collecting data. The procedure of the slaughter was described in

Chapter 3. After slaughtering, the carcasses were stored at 4º C for 24 hours and then, in the meat laboratory of the Department of Animal Science of the UPV, the *Longissimus* muscles (LM) were excised from the carcasses.

6.3.3 Meat quality traits.

Muscle pH at 24 h. *post mortem* was measured in the LM muscle at the site of the fifth lumbar vertebra on the left side and recorded with a Crison pH-meter Basic 20+ (Crison Instruments, Barcelona, Spain). Meat colour (lightness, L*; redness, a*; and yellowness, b*) was measured at the seventh lumbar vertebra in a transversal section of the right LM. Meat obtained from the LM was ground, freeze-dried and stored at -80º C until analyses. Meat was scanned with near infrared reflectance spectroscopy (NIRS) (model 5000, FOSS NIRSystems INC., Hilleroed, Denmark). Protein content and fatty acid (FA) composition of the LM were determined applying calibration equations previously developed (Zomeño et al., 2012).

6.3.4 Data Recording and Statistical Model.

The pH was measured in a total of 950 LM which came from carcasses that were used in Chapter 3 and the other meat quality traits were recorded in a sample of 285 LM of these animals.

The model used in the analysis was:

$$Y_{jkl} = GG_j + F_k + S_l + e_{jkl}$$

Where: Y_{jkl} 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_l is the effect of the sex and e_{jkl} is the residual effect.

Estimates of the differences between all the genetics groups and VV animals were obtained by least-squares, using the program blupf90 (Misztal et al., 2002). In addition to the estimates, the error (co)variance matrix between these estimates was obtained. The 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 were obtained from a full diallel cross among four maternal lines, and all their sires were of the same paternal line (R line). Thus, there were five 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 ($G_i^{M'}$, 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 are not estimable individually, but the following functions of them are estimable:

d) Direct-maternal differences between lines**,**

$G_{i-j}^I = 1/2(G_i^D - G_j^D) + (G_i^M - G_j^M) + (H_{Ri}^I - H_{Rj}^I)$**,** i ≠ j, i = A, V, H, L and j =A, V, H, L

e) Grand-maternal differences between lines, ($G_{i-j}^{M'} = G_i^{M'} - G_j^{M'}$) , i ≠ j, i = A, V, H, L and j=A, V, H, L

f) Maternal heterosis, previously defined.

Estimable functions of the crossbreeding parameters were obtained adjusting by generalized least-squares the estimates of the genetic groups effects (as contrasts to the V line) to the coefficients described in Chapter 2. In this generalized 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.

6.4 RESULTS AND DISCUSSION.

6.4.1 Descriptive Statistics.

Summary statistics are shown in Tables 1 and 2 for pH, colour, protein content (g/100g muscle) and fatty acid group composition (g/100g muscle) of the LM, and in Table 3 for individual fatty acid composition (mg/100g muscle) of the LM. The value for pH was similar to those obtained in previous studies (Hernández et al., 2004; Hernández

Table 1. Descriptive statistics of pH, colour, intramuscular fat (IMF, g/100g muscle) and protein (g/100g muscle) of the *Longissimus* muscle (LM).

Trait[1]	N[2]	Mean	SD[3]	Minimum	Maximum
pH	950	5.66	0.17	5.05	6.20
L*	285	51.52	3.37	39.07	59.89
a*	285	4.69	1.44	1.97	9.72
b*	285	1.61	1.44	-1.80	6.97
IMF	285	1.21	0.22	0.80	2.09
Protein	285	22	0.40	20	23

[1] . L*= lightness of the *longissimus* muscle. a*= redness of the *longissimus* muscle. b*= yellowness of the *longissimus* muscle. [2] N= number of LM.[3] SD= standard deviation.

Table 2. Descriptive statistics of fatty acid groups (mg/100 g. muscle) and fatty acid ratios of the *Longissimus* muscle (LM).

Trait[1]	N[2]	Mean	SD[3]	Minimum	Maximum
SFA	285	308	66	173	546
MUFA	285	232	70	99	491
PUFA	285	331	36	243	449
n-3 PUFA	285	54	3	47	66
n-6 PUFA	285	277	35	208	409
n-6/n-3	285	5.10	0.47	3.94	7.95
PUFA/SFA	285	1.09	0.08	0.84	1.29

[1] . SFA= C14:0+C15:0+C16:0+C17:0+C18:0; MUFA= C16:1+C18:1n-9+C18:1n-7; PUFA=C18:2n-6+C18:3n-3+C20:2n-6+C20:3n-6+C20:4n-6+C20:5n-3+C22:4n-6+C22:5n-3+C22:6n-3; n-3= C18:3n-3+C20:5n-3+C22:5n-3+C22:6n-3; n-6= C18:2n-6+C20:2n-6+C20:3n-6+C20:4n-6+C22:4n-6; [2] N= number of LM; [3] SD= standard deviation.

and Gondret, 2006; Zomeño, 2013) and is in within the optimum range to avoid potentials problems related with meat pH. In rabbit, pH ranges between 5.4 and 6.4, depending on muscle location (Hulot and Ouhayoun, 1999), but it did not appear that a potential problem existed for meat quality. To date, the literature has not reported any abnormal port-mortem acidification kinetics characteristics or pale, soft and exudative (PSE) or acid meat in rabbit meat (Hernández and Dalle Zotte, 2010).

Table 3. Descriptive statistics of individual fatty acid composition (mg/100 g muscle) of the *Longissimus* muscle (LM).

Trait	N[1]	Mean	SD[2]	Min[3]	Max[4]
C14:0 (myristic)	285	14.2	5.2	1.0	32.0
C15:0 (pentadecanoic)	285	4.3	0.9	2.6	7.8
C16:0 (palmitic)	285	200	45	119	387
C16:1 (palmitoleic)	285	15.8	9.7	3.3	56.7
C17:0 (heptadecanoic)	285	6.0	1.1	3.6	10.5
C18:0 (stearic)	285	70	9	52	108
C18:1 n-7(vaccenic)	285	14.1	2.3	9.4	23.4
C18:1 n-9 (oleic)	285	192	54	90	402
C18:2 n-6 (linoleic)	285	196	36	124	326
C18:3 n-3 (linolenic)	285	14.0	4.4	4.6	30.1
C20:2 n-6 (eicosadienoic)	285	2.6	0.6	1.9	4.2
C20:3 n-6 (eicosatrienoic)	285	4.2	0.4	3.3	7.7
C20:4 n-6 (arachidonic)	285	45.9	2.5	29.3	51.7
C20:5 n-3 (eicosapentanoic)	285	12.4	1.5	7.4	16.2
C22:4 n-6 (docosatetraenoic)	285	16.5	0.4	15.4	19.3
C22:5 n-3 (docosapentanoic)	285	6.4	0.8	1.8	10.0
C22:6 n-3 (docosahexanoic)	285	21.0	2.5	4.6	27.5

[1]. N= number of LM. [2]. SD= standard deviation [3]. Min= minimum [4]. Max= maximum

Combes and Dalle Zotte (2005) showed that the main meats consumed (pork, chicken, beef, lamb) are in the same ranges of values. Colour variables were also in the range of that reported by Hernández et al. (2004), Combes and Dalle Zotte (2005), Hernández and Gondret (2006) and Zomeño (2013). Rabbit meat has a high lightness (L*) because it has a high capacity to reflect the light and due to its low myoglobin content it has a low red index (a*).

Rabbit meat ranks first in lightness when compared to white meats, such as turkey and chicken in similar muscles, and with respect to redness it ranks third after pork and turkey (Dalle Zotte, 2004). Intramuscular fat (IMF) showed a low value because LM is the leanest muscle of the carcass (Pla et al., 2004). Fat and protein values are in the ranges already reported by Metzger et al. (2003), Pla et al. (2004), Hernández and Dalle Zotte (2010) and Zomeño (2013). The main FA groups in rabbit LM were polyunsaturated (PUFA) and saturated (SFA) with percentages around 37 and 36% of total FA, respectively. Monounsaturated (MUFA) FA represented a lower percentage (27%). Among PUFA, n-6 was the most abundant with percentage of 32%, while n-3 had a percentage of 6%. These values are in the same magnitude of those reported by Hernandez and Dalle Zotte (2010), Dalle Zotte and Szendro (2011) and Zomeño et al. (2012). PUFA/SFA and n-6/n-3 ratios, used to evaluate quality of fat, showed values close to the nutritional recommendations (reviewed by Hernández and Dalle Zotte, 2010).

As shown in Table 3, the most abundant FA in LM were palmitic (C16:0), oleic (C18:1 n-9) and linoleic (C18:2 n-6) acids, showing percentages of 24, 23 and 23%, respectively. Stearic (C18:0) and arachidonic acids (C20:4 n-6) were also important with percentages around 8 and 5%, respectively. Linolenic acid (C18:3 n-3) and some long chain PUFA (i.e. C20:5 n-3, C22:4 n-6 and C22:6 n-3) were also present in rabbit

meat although at a lower content. The FA composition in LM observed was similar to that reported in previous studies (reviewed by Hernández and Gondret, 2006; Zomeño et al., 2012).

6.4.2 Differences between genetic groups.

In Tables 4 and 5, contrasts due to dam effects of the lines for pH, colour, intramuscular fat (IMF, g./100g muscle), protein (g./100g muscle), fatty acid groups (mg/100 g muscle) and fatty acid ratios of the LM can be observed. Tables 6 and 7 show the same contrasts for individual fatty acid composition (mg/100 g muscle). Notice that when the lines involved in the contrast do not share the farm (H line with A and LP lines) have higher standard errors, as expected. Muscle pH exerts a high influence on the technological and eating quality of meat. The post-mortem development of pH and the pH measured at 24 h post-mortem affect the brightness of meat, its water holding capacity and toughness (Lawrie, 1998) and an abnormal postmortem acidification can produce PSE or DFD meat. A significant difference was observed between A and LP lines, but this difference, and the others which were not significant, were not relevant because all lines were in the range of an appropriate pH. Hernández and Gondret (2006) studied pH differences between A and V lines and did not observe differences between them. Meat colour affects consumer acceptance and purchasing decisions (Hernández and Dalle Zotte, 2010). Significant differences were not observed in the contrasts between lines for L*, a* and b*. Notice that, in Chapter 3 we observed significant differences for a* and b* (A-V, H-V and LP-V, in favor of the V line) for carcass colour, although these differences did not appear for meat colour. IMF plays an essential role in meat quality, largely determining eating quality and the nutritional value of the meat (Wood et al., 2008). Regarding IMF, the line A had the higher

content, being significant for the difference with respect to line V. Rabbit meat is rich in proteins compared to other meats, and also contains high levels of essential amino acids of high digestibility (Hernández and Dalle Zotte, 2010). Non-significant differences were found for the content of protein between the lines. One of the main aims of meat researchers is to produce dietetic and healthy meat to reduce the SFA and increase the unsaturated FA (Dalle Zotte, 2002). Thus, it is important to measure the possible differences between lines for these traits. Significant differences in the contrast A-V were found for all fatty acid groups (in favor of the A line), and despite non-significant differences with the other lines, it seemed that line A had the highest content for fatty acid groups (SFA, MUFA and PUFA) in agreement with its highest value for IMF. Among PUFA, significant differences were shown between A-V for n-3 PUFA and between A-V and A-LP for n-6 PUFA (in favor of the A line). Although, no other contrasts for fatty acid group content involving line A were significant, it appeared that this line has the highest values. The Department of Health and Social Security (1994) recommended a ratio of 0.45 or higher for PUFA/SFA and a maximum of 4.0 for the n-6/n-3 ratio. However, diets in developed countries seem to have much higher n-6/n-3 ratios fatty acids than in n-3 fatty acids, and the PUFA/SFA ratios are far from the recommended value. For ratios n-6/n-3 and PUFA/SFA, no significant differences were found between the lines, and the four lines have acceptable values for the first ratio and a slight excess of n-6 in the second (Table 2). Tables 6 and 7 show significant differences in the contrast A-V, in favor of the A line, for SFA (C14:0, C15:0, C16:0, C17:0 and C18:0), MUFA (C16:1, C18:1n-9 and C18:1n-7) and C18:2 n-6, C18:3 n-3 and C20:2 n-6. Significant differences were not found between the A and the other lines, but it seemed that this line had the highest values for all traits, as previously mentioned for IMF, and fatty acid groups (Tables 4 and 5).

Table 4. Contrasts (standard error) between the lines for pH, colour, intramuscular fat (IMF, g/100g muscle) and protein (g/100g muscle) of the *Longissimus* muscle.

Trait[1]	A-H	A-LP	A-V	H-V	LP-H	LP-V
pH	0(0.03)	0.05(0.02)*	0.04(0.02)	0.04(0.02)	-0.06(0.03)	-0.02(0.02)
L*	-0.78(1.50)	-0.44(1.07)	-0.14(1.09)	0.64(1.03)	-0.34(1.47)	0.30(1.05)
a*	0.79(0.66)	0(0.47)	-0.20(0.48)	-1.00(0.45)	0.78(0.65)	-0.21(0.46)
b*	0.03(0.55)	-0.12(0.40)	0.08(0.41)	0.05(0.40)	0.15(0.56)	0.20(0.40)
IMF	0.15(0.11)	0.14(0.08)	0.23(0.08)*	0.08(0.08)	0.01(0.11)	0.09(0.08)
Protein	-0.10(0.20)	0.05(0.14)	0.17(0.15)	0.27(0.14)	-0.15(0.20)	0.13(0.15)

[1] . L*= lightness of the *longissimus* muscle. a*= redness of the *longissimus* muscle. b*= yellowness of the *longissimus* muscle. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 5. Contrasts (standard error) between the lines for fatty acid groups (mg/100 g muscle) and fatty acid ratios of the *Longissimus* muscle.

Trait[1]	A-H	A-LP	A-V	H-V	LP-H	LP-V
SFA	49(33)	38(23)	67(24)*	19(23)	10(33)	29(24)
MUFA	58(33)	41(23)	66(24)*	8(23)	17(33)	25(24)
PUFA	26(18)	24(13)	34(13)*	7(13)	3(18)	10(13)
n-3 PUFA	2.4(1.6)	2.1(1.1)	3.1(1.1)*	0.7(1.1)	0.2(1.6)	0.9(1.1)
n-6 PUFA	26(18)	25(13)*	31(13)*	4(12)	1(13)	5(12)
n-6/n-3	0.41(0.24)	0.22(0.16)	0.25(0.16)	-0.16(0.16)	0.19(0.24)	0.03(0.16)
PUFA/SFA	-0.05(0.04)	-0.02(0.02)	-0.05(0.03)	0(0.02)	-0.02(0.04)	-0.02(0.03)

[1] . SFA= C14:0+C15:0+C16:0+C17:0+C18:0. MUFA= C16:1+C18:1n-9+C18:1n-7. PUFA=C18:2n-6+C18:3n-3+C20:2n-6+C20:3n-6+C20:4n-6+C20:5n-3+C22:4n-6+C22:5n-3+C22:6n-3. n-3= C18:3n-3+C20:5n-3+C22:5n-3+C22:6n-3. n-6= C18:2n-6+C20:2n-6+C20:3n-6+C20:4n-6+C22:4n-6.

*$P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 6. Contrasts (standard error) between the lines for SFA and MUFA composition (mg/ 100 g muscle) of the *Longissimus* muscle.

Trait[1]	A-H	A-LP	A-V	H-V	LP-H	LP-V
C14:0	3.0(2.6)	2.5(1.8)	5.6(1.9)*	2.5(1.8)	0.5(2.6)	3.1(1.9)
C15:0	0.7(0.4)	0.5(0.3)	0.9(0.3)*	0.2(0.3)	0.1(0.4)	0.3(0.3)
C16:0	31(22)	22(15)	41(16)*	10(15)	9(22)	19(16)
C16:1	7.1(4.7)	7.4(3.2)	10.0(3.3)*	2.7(3.2)	2.6(4.7)	5.4(3.3)
C17:0	0.9(0.6)	0.7(0.4)	0.9(0.4)*	0.0(0.4)	0.3(0.6)	0.2(0.4)
C18:0	6.9(4.7)	6.2(3.3)	9.4(3.4)*	2.6(3.3)	0.7(4.7)	3.3(3.4)
C18:1 n-7	1.6(1.2)	1.5(0.8)	2.3(0.8)*	0.6(0.8)	0.2(1.2)	0.8(0.8)
C18:1 n-9	47(27)	33(19)	53(19)*	6(19)	13(27)	19(19)

[1]. C14:0 = myristic acid, C15:0 = pentadecanoic acid, C16:0 = palmitic acid, C16:1 = palmitoleic acid, C17:0 = heptadecanoic acid, C18:0 = stearic acid, C18:1 n-7 = vaccenic acid, C18:1 n-9 = oleic acid.. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 7. Contrasts (standard error) between the lines for PUFA composition (mg/ 100 g muscle) of the *Longissimus* muscle.

Trait[1]	A-H	A-LP	A-V	H-V	LP-H	LP-V
C18:2 n-6	33(18)	24(13)	32(13)*	-1(13)	9(18)	8(13)
C18:3 n-3	4.3(2.2)	2.7(1.5)	4.0(1.6)*	-0.3(1.5)	1.6(2.2)	1.3(1.6)
C20:2 n-6	0.3(0.2)	0.2(0.1)	0.3(0.1)*	0.0(0.1)	0.1(0.2)	0.1(0.1)
C20:3 n-6	0.2(0.2)	0(0.1)	0(0.1)	-0.2(0.1)	0.2(0.2)	0.1(0.1)
C20:4 n-6	-1(1)	0.7(1)	0(1)	1(1)	-1(1)	0(1)
C20:5 n-3	-0.3(0.6)	-0.3(0.4)	-0.1(0.4)	0.2(0.4)	0.0(0.6)	0.2(0.4)
C22:4 n-6	-0.1(0.2)	-0.1(0.1)	-0.2(0.1)	0.2(0.1)	0(0.2)	0.2(0.1)
C22:5 n-3	0.0(0.4)	0.5(0.3)	0.1(0.3)	0.2(0.3)	-0.1(0.4)	0.1(0.3)
C22:6 n-3	-1.6(1.5)	0.1(1.0)	0.3(1.0)	1.9(1.1)	-1.7(1.5)	0.2(1.0)

[1]. C18:2 n-6 = linoleic acid, C18:3 n-3 = linolenic acid, C20:2 n-6 = eicosadienoic acid, C20:3 n-6 = eicosatrienoic acid, C20:4 n-6 = arachidonic acid, C20:5 n-3 = eicosapentanoic acid, C22:4 n-6 = docosatetraenoic acid, C22:5 n-3 = docosapentanoic acid, C22:6 n-3 = docosahexanoic acid**.** *$P < 0.05$ (significant difference at $\alpha = 0.05$).

On commercial farms, crossbred does are the most common type of females and, consequently, some differences in meat quality traits in dam effects might impart some importance. As we stated in Chapters 2 and 3 for growth traits and carcass traits, respectively, we consider first the different crossbred groups (the average of a cross and its reciprocal) with respect to the V line. In Tables 8 and 9 the contrasts due to dam effects of the lines for pH, colour, intramuscular fat (IMF, g/100g muscle), protein (g/100g muscle), fatty acid groups (mg/100 g muscle) and fatty acid ratios of the LM can be observed. In general, no significant differences were found in the contrast All-VV. Only for a* was this contrast significant in favor of the V line. Also for a*, the contrasts AH-VV and AL-VV were significant asowing superiority for line V. Presented in Tables 8 and 9, crossbreds involving the A line had the higher content for IMF, SFA, MUFA, PUFA, n-3 PUFA, n-6 PUFA with respect to purebred V animals (significant differences exisited only between AH and VV). This result agrees with those previously mentioned as found in the Tables 4 and 5. Tables 10 and 11 showed no significant differences for individual fatty acids in the contrast All-VV. In agreement with Table 9, results found in Tables 10 and 11 indicated that the contrast AH-VV was significant for SFA (C14:0, C15:0, C16:0 and C18:0), MUFA (C16:1, C18:1n-9 and C18:1n-7) and C18:3 n-3 in favor of the crossbred AH. However, C22:4 n-6 was higher for animals from purebred V dams than for animals from AH dams.

Table 8. Contrasts (standard error) between crossbred genetic groups[1] and V line for pH, colour, intramuscular fat (IMF, g/100g muscle) and protein (g/100g muscle) of the *Longissimus* muscle.

Trait[2]	AH-VV	AL-VV	AV-VV	HV-VV	LH-VV	LV-VV	All-VV
pH	0.04(0.02)	0.03(0.02)	0(0.02)	0(0.02)	0(0.02)	0(0.02)	0.01(0.01)
L*	0.41(0.69)	-0.31(0.70)	0.44(0.70)	0.14(0.71)	-0.52(0.71)	-0.32(0.70)	-0.02(0.53)
a*	-0.64(0.30)*	-0.61(0.31)*	-0.44(0.31)	-0.55(0.31)	-0.40(0.31)	-0.19(0.31)	-0.47(0.23)*
b*	-0.40(0.26)	-0.58(0.27)	-0.21(0.27)	-0.03(0.27)	-0.26(0.27)	-0.18(0.27)	-0.27(0.20)
IMF	0.15(0.05)*	0.05(0.05)	0.2(0.05)	0.06(0.05)	0.07(0.05)	-0.06(0.05)	0.05(0.04)
Protein	0.1(0.1)	0(0.1)	0(0.1)	0(0.1)	0(0.1)	0.1(0.1)	0(0.1)

[1]. One cross and its reciprocal are considered together. [2]. L*= lightness of the *longissimus* muscle. a*= redness of the *longissimus* muscle. b*= yellowness of the *longissimus* muscle. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 9. Contrasts (standard error) between crossbred genetic groups[1] and V line for fatty acid groups (mg/100 g muscle) and fatty acid ratios of the *Longissimus* muscle.

Trait[2]	AH-VV	AL-VV	AV-VV	HV-VV	LH-VV	LV-VV	All-VV
SFA	47(16)*	17(16)	8(16)	19(16)	24(16)	-18(16)	16(12)
MUFA	40(16)*	13(16)	2(16)	16(16)	16(16)	-18(16)	11(12)
PUFA	20(9)*	4(9)	0(9)	7(9)	6(9)	-10(9)	4(6)
n-3 PUFA	2.1(0.8)*	0.7(0.8)	0.2(0.8)	0.7(0.8)	1.0(0.8)	-0.8(0.8)	0.6(0.6)
n-6 PUFA	19(9)*	6(9)	-1(9)	10(9)	12(9)	-4(9)	6(7)
n-6/n-3	0.1(0.1)	0(0.1)	-0.1(0.1)	0(0.1)	0(0.1)	-0.1(0.1)	0(0.1)
PUFA/SFA	-0.03(0.02)	0(0.02)	-0.02(0.02)	-0.01(0.02)	-0.01(0.02)	0.02(0.02)	-0.01(0.01)

[1] . One cross and its reciprocal are considered together. [2] . SFA= C14:0+C15:0+C16:0+C17:0+C18:0. MUFA= C16:1+C18:1n-9+C18:1n-7. PUFA=C18:2n-6+C18:3n-3+C20:2n-6+C20:3n-6+C20:4n-6+C20:5n-3+C22:4n-6+C22:5n-3+C22:6n-3. n-3= C18:3n-3+C20:5n-3+C22:5n-3+C22:6n-3. n-6= C18:2n-6+C20:2n-6+C20:3n-6+C20:4n-6+C22:4n-6. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 10. Contrasts (standard error) between crossbred genetic groups[1] and V line for SFA and MUFA composition (mg/ 100 g muscle) of the *Longissimus* muscle.

Trait[2]	AH-VV	AL-VV	AV-VV	HV-VV	LH-VV	LV-VV	All-VV
C14:0	3.71(1.28)*	1.74(1.29)	0.29(1.29)	1.36(1.30)	1.86(1.31)	-1.21(1.30)	1.28(0.99)
C15:0	0.51(0.21)*	0.14(0.21)	0.03(0.21)	0.23(0.21)	0.20(0.21)	-0.23(0.21)	0.15(0.16)
C16:0	26(10)*	11(10)	8(10)	13(10)	19(10)	-12(10)	11(8)
C16:1	6.7(2.3)*	2.9(2.3)	1.1(2.3)	3.2(2.3)	4.1(2.3)	-2.0(2.3)	2.6(1.7)
C17:0	0.4(0.3)	0.1(0.3)	-0.1(0.3)	0.1(0.3)	0.2(0.3)	-0.3(0.3)	0.1(0.2)
C18:0	5.6(2.3)*	1.5(2.3)	0.0(2.3)	1.7(2.3)	2.0(2.3)	-2.6(2.3)	1.5(1.7)
C18:1 n-7	1.4(0.6)*	0.4(0.6)	0.0(0.6)	0.7(0.6)	0.5(0.6)	-0.6(0.6)	0.4(0.4)
C18:1 n-9	32(13)*	10(13)	1(13)	12(13)	13(13)	-15(13)	9(10)

[1]. One cross and its reciprocal are considered together. [2]. C14:0 = myristic acid, C15:0 = pentadecanoic acid, C16:0 = palmitic acid, C16:1 = palmitoleic acid, C17:0 = heptadecanoic acid, C18:0 = stearic acid, C18:1 n-7 = vaccenic acid, C18:1 n-9 = oleic acid. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 11. Contrasts (standard error) between crossbred genetic groups[1] and V line for PUFA composition (mg/ 100 g muscle) of the *Longissimus* muscle.

Trait[2]	AH-VV	AL-VV	AV-VV	HV-VV	LH-VV	LV-VV	All-VV
C18:2 n-6	16(9)	7(9)	-1(9)	6(9)	11(9)	-7(9)	5(7)
C18:3 n-3	2.1(1.1)*	1.0(1.1)	0.1(1.1)	0.9(1.1)	1.5(1.1)	-0.8(1.1)	0.8(0.8)
C20:2 n-6	0.1(0.1)	0.1(0.1)	0.0(0.1)	0.0(0.1)	0.1(0.1)	-0.1(0.1)	0.1(0.1)
C20:3 n-6	0.0(0.1)	0.1(0.1)	-0.1(0.1)	0.0(0.1)	0.0(0.1)	0.0(0.1)	0.0(0.1)
C20:4 n-6	0.3(0.6)	-0.2(0.6)	-0.2(0.6)	-0.8(0.6)	-0.3(0.6)	-1.0(0.6)	0.3(0.4)
C20:5 n-3	0.0(0.3)	-0.1(0.3)	0.0(0.3)	0.1(0.3)	-0.1(0.3)	0.2(0.3)	0.1(0.2)
C22:4 n-6	-0.3(0.1)*	-0.2(0.1)	-0.1(0.1)	-0.1(0.1)	-0.3(0.1)*	-0.1(0.1)	-0.2(0.1)
C22:5 n-3	-0.1(0.2)	-0.1(0.2)	0.1(0.2)	-0.1(0.2)	-0.2(0.2)	-0.3(0.2)	-0.1(0.2)
C22:6 n-3	-0.2(0.7)	-0.5(0.7)	-0.1(0.7)	-0.8(0.7)	-1.0(0.7)	-1.0(0.7)	-0.6(0.6)

[1] . One cross and its reciprocal are considered together. [2]. C18:2 n-6 = linoleic acid, C18:3 n-3 = linolenic acid, C20:2 n-6 = eicosadienoic acid, C20:3 n-6 = eicosatrienoic acid, C20:4 n-6 = arachidonic acid, C20:5 n-3 = eicosapentanoic acid, C22:4 n-6 = docosatetraenoic acid, C22:5 n-3 = docosapentanoic acid, C22:6 n-3 = docosahexanoic acid. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

The importance of using a particular line, either as sire or dam, in a cross was assessed by testing the differences between a particular cross and its reciprocal (Tables 12, 13, 14 and 15). A given cross and its reciprocal were raised on different farms, but connected by the line V that was raised on all the farms. The consequence of this is that the standard errors of the contrasts for the reciprocal effect (Tables 12, 13, 14 and 15) were higher than for the contrasts between the lines raised on the same farm and for the average of a cross and its reciprocal with respect to line V. In Table 12, a significant difference was found in the contrast HV-VV for a* in favor of the line V as sire. In Table 13, for the contrast AV-VA the significant difference in SFA was favorable to the A line acting as sire, because the crossbred AV had a lower value of SFA than VA animals, and, as previously stated, one desirable feature would be to reduce the level of SFA.

Table 14 shows significant differences for C16:0 and C16:1 in the contrast AV-VA (higher values for VA). The higher value of C16:0 in the cross VA fully agrees with the results in Table 13 of this cross having higher level of SFA. In addition, Table 15 also shows significant differences in the contrast AH-HA for C20:5n-3 (in favor of H as sire) and for C22:5n-3 (in favor of A as sire). These results and the remaining contrasts between the reciprocal crosses; however show that the situation is not clear, making it difficult to decide if one cross or its reciprocal is the best or optimal because, in general, the reciprocal effects are infrequent and does not follow a clear or consistent pattern.

Table 12. Contrasts (standard error) between reciprocal crosses for pH, colour, intramuscular fat (IMF, g/100g muscle) and protein (g/100g muscle), of the *Longissimus* muscle.

Trait[1]	AH-HA	AL-LA	AV-VA	HV-VH	LH-HL	LV-VL
pH	0.04(0.03)	-0.02(0.03)	-0.01(0.03)	-0.02(0.03)	-0.06(0.03)	-0.04(0.03)
L*	-1.6(1.4)	1.4(1.4)	0.4(1.4)	2.0(1.4)	2.4(1.4)	0.3(1.4)
a*	-0.2(0.6)	0.2(0.6)	0.1(0.6)	-1.3(0.6)*	-0.4(0.6)	0.5(0.6)
b*	-0.8(0.05)	0.5(0.05)	0.4(0.05)	0.5(0.05)	-0.3(0.05)	0.3(0.05)
IMF	0.1(0.1)	-0.1(0.1)	-0.2(0.1)	0.1(0.1)	0.1(0.1)	0.0(0.1)
Protein	0.1(0.2)	0.1(0.2)	0(0.2)	-0.2(0.2)	0.2(0.2)	0.1(0.2)

[1]. L*= lightness of the *longissimus* muscle. a*= redness of the *longissimus* muscle. b*= yellowness of the *longissimus* muscle. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 13. Contrasts (standard error) between reciprocal crosses for fatty acid groups (mg/100 g muscle) and fatty acid ratios of the *Longissimus* muscle.

Trait[1]	AH-HA	AL-LA	AV-VA	HV-VH	LH-HL	LV-VL
SFA	46(32)	-18(32)	-70(32)*	41(32)	25(32)	-8(32)
MUFA	40(33)	-17(33)	-58(33)	32(33)	22(33)	-3(33)
PUFA	17(18)	-8(18)	-29(18)	15(18)	10(18)	-3(18)
n-3 PUFA	2.5(1.6)	-1.3(1.6)	-2.9(1.6)	1.4(1.6)	1.1(1.6)	-1.0(1.6)
n-6 PUFA	15(17)	0(17)	-25(17)	19(17)	6(17)	-1(17)
n-6/n-3	0(0.2)	0(0.2)	-0.1(0.2)	0.1(0.2)	0.1(0.2)	0.2(0.2)
PUFA/SFA	-0.06(0.04)	0.03(0.04)	0.06(0.04)	-0.03(0.04)	-0.02(0.04)	0.00(0.04)

[1] . SFA= C14:0+C15:0+C16:0+C17:0+C18:0. MUFA= C16:1+C18:1n-9+C18:1n-7. PUFA=C18:2n-6+C18:3n-3+C20:2n-6+C20:3n-6+C20:4n-6+C20:5n-3+C22:4n-6+C22:5n-3+C22:6n-3. n-3= C18:3n-3+C20:5n-3+C22:5n-3+C22:6n-3. n-6= C18:2n-6+C20:2n-6+C20:3n-6+C20:4n-6+C22:4n-6. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 14. Contrasts (standard error) between reciprocal crosses for SFA and MUFA composition (mg/ 100 g muscle) of the *Longissimus* muscle.

Trait[1]	AH-HA	AL-LA	AV-VA	HV-VH	LH-HL	LV-VL
C14:0	2.9(2.6)	-1.5(2.6)	-4.9(2.6)	2.5(2.6)	1.8(2.6)	0.0(2.6)
C15:0	0.5(0.4)	-0.2(0.4)	-0.7(0.4)	0.4(0.4)	0.6(0.4)	-0.3(0.4)
C16:0	32(21)	-13(21)	-45(21)*	26(21)	8(21)	-9(21)
C16:1	6.8(4.6)	-3.3(4.6)	-9.7(4.6)*	4.3(4.6)	3.0(4.6)	-3.1(4.6)
C17:0	0.6(0.6)	-0.2(0.6)	-0.8(0.6)	0.7(0.6)	0.2(0.6)	0.0(0.6)
C18:0	5.0(4.6)	-2.5(4.6)	-8.0(4.6)	4.5(4.6)	2.7(4.6)	-0.6(4.6)
C18:1 n-7	1.0(1.2)	-0.5(1.2)	-1.9(1.2)	1.1(1.2)	0.6(1.2)	-0.3(1.2)
C18:1 n-9	-33(26)	-14(26)	-48(26)	27(26)	18(26)	-2(26)

[1]. C14:0 = myristic acid, C15:0 = pentadecanoic acid, C16:0 = palmitic acid, C16:1 = palmitoleic acid, C17:0 = heptadecanoic acid, C18:0 = stearic acid. C18:1 n-7 = vaccenic acid, C18:1 n-9 = oleic acid. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 15. Contrasts (standard error) between reciprocal crosses for PUFA composition (mg/ 100 g muscle) of the *Longissimus* muscle.

Trait[1]	AH-HA	AL-LA	AV-VA	HV-VH	LH-HL	LV-VL
C18:2 n-6	15(18)	-3(18)	-25(18)	18(18)	5(18)	-2(18)
C18:3 n-3	2.0(2.2)	-0.4(2.2)	-3.3(2.2)	2.3(2.2)	0.7(2.2)	-0.6(2.2)
C20:2 n-6	0.1(0.2)	0.1(0.2)	-0.2(0.2)	0.1(0.2)	-0.1(0.2)	-0.1(0.2)
C20:3 n-6	-0.2(0.2)	0.2(0.2)	0.0(0.2)	0.1(0.2)	-0.1(0.2)	0.3(0.2)
C20:4 n-6	2.2(1.2)	-1.6(1.2)	-1.3(1.2)	-0.1(1.2)	0.6(1.2)	-0.3(1.2)
C20:5 n-3	-1.6(0.5)*	0.4(0.5)	0.3(0.5)	0.0(0.5)	0.2(0.5)	0.0(0.5)
C22:4 n-6	0.1(0.2)	-0.2(0.2)	0.1(0.2)	0.1(0.2)	0.1(0.2)	0.0(0.2)
C22:5 n-3	1.00(0.4)*	-0.2(0.4)	-0.5(0.4)	0.0(0.4)	0.3(0.4)	-0.6(0.4)
C22:6 n-3	1.0(1.5)	-1.0(1.5)	0.0(1.5)	-0.2(1.5)	-0.1(1.5)	-0.4(1.5)

[1]. C18:2 n-6 = linoleic acid, C18:3 n-3 = linolenic acid, C20:2 n-6 = eicosadienoic acid, C20:3 n-6 = eicosatrienoic acid, C20:4 n-6 = arachidonic acid, C20:5 n-3 = eicosapentanoic acid, C22:4 n-6 = docosatetraenoic acid, C22:5 n-3 = docosapentanoic acid, C22:6 n-3 = docosahexanoic acid.*$P < 0.05$ (significant difference at $\alpha = 0.05$).

6.4.3 Direct-maternal effects.

Differences between direct-maternal effects are shown in Tables 16, 17, 18 and 19. The results of the contrasts between lines (Tables 4, 5, 6 and 7) are in close agreement with the results for direct-maternal differences between lines. For pH, significant differences were found for G^I_{A-V}, G^I_{L-H} and G^I_{L-V} (negative values). These indicate direct-maternal effects of the LP line are the lowest relative to other lines.

The similarity for the significant differences between the contrasts between lines (Tables 4 and 5) and the contrast for direct-maternal effects (16 and 17) is complete for IMF, SFA, MUFA, PUFA, n-3 PUFA and n-6 PUFA. Thus, G^I_{A-V} was significant for these traits. According to resuts in Tables 4 and 5, here G^I_{A-H} and G^I_{A-L} had positive values (but no significant differences) and there were indications that the direct-maternal effects of the A line were the highest. In Tables 18 and 19, significant differences were found in G^I_{A-V} for C14:0, C15:0, C16:1, C17:0, C18:0 C18:1n-7, C18:1n-9, C18:2n-6 and C18:3 n-3 in favor of the A line. These results agree with those previously discussed from Tables 6 and 7. For C16:0, C17:0, C18:1n-7 and C20:2n-6, no significant differences were found regarding G^I_{A-V}; however, these results do not agree with those from Tables 6 and 7, but they did show the same pattern. For G^I_{A-H} and G^I_{A-L}, there were no significant differences but, as seen previouslyin Table 4, there are indications that the direct-maternal effects of the A line were the highest.

Table 16. Direct-maternal effect differences between lines[1] (standard error) for pH, colour, intramuscular fat (IMF, g/100g muscle) and protein (g/100g muscle) of the *Longissimus* muscle.

Trait[2]	[1] G^I_{A-H}	G^I_{A-L}	G^I_{A-V}	G^I_{H-V}	G^I_{L-H}	G^I_{L-V}
pH	0.00(0.04)	0.08(0.03)*	0.02(0.03)	0.02(0.03)	-0.08(0.04)*	-0.06(0.03)*
L*	-1.35(1.6)	-0.82(1.3)	0.22(1.3)	1.58(1.3)	-0.53(1.6)	1.05(1.3)
a*	1.20(0.72)	-0.06(0.56)	-0.19(0.56)	-1.39(0.56)*	1.26(0.72)	-0.13(0.56)
b*	-0.39(0.63)	-0.10(0.48)	0.31(0.48)	0.71(0.48)	-0.29(0.63)	0.41(0.48)
IMF	0.14(0.12)	0.11(0.10)	0.20(0.10)*	0.06(0.10)	0.03(0.12)	0.09(0.10)
Protein	-0.01(0.23)	-0.05(0.18)	0.11(0.18)	0.13(0.18)	-0.04(0.23)	0.17(0.18)

[1]. G^I_{i-j} = direct-maternal differences between lines i and j (see text for a complete explanation). [2]. L*= lightness of the *longissimus* muscle. a*= redness of the *longissimus* muscle. b*= yellowness of the *longissimus* muscle. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 17. Direct-maternal effect differences between lines[1] (standard error) for acid groups (mg/100 g muscle) and fatty acid ratios of the *Longissimus* muscle.

Trait[2]	[1] G^I_{A-H}	G^I_{A-L}	G^I_{A-V}	G^I_{H-V}	G^I_{L-H}	G^I_{L-V}
SFA	45(37)	33(29)	63(29)*	17(29)	12(37)	30(29)
MUFA	56(37)	34(29)	61(29)*	4(29)	22(37)	26(29)
PUFA	24(20)	20(16)	33(16)*	5(16)	4(20)	9(16)
n-3 PUFA	2.4(1.8)	2.2(1.4)	2.9(1.4)*	0.2(1.4)	0.4(1.8)	0.6(1.4)
n-6 PUFA	24(20)	26(15)	31(15)*	7(15)	-2(20)	5(15)
n-6/n-3	0.4(0.3)	0.1(0.2)	0.3(0.2)	-0.1(0.2)	0.3(0.3)	0.2(0.2)
PUFA/SFA	-0.06(0.04)	-0.02(0.03)	-0.05(0.03)	0.00(0.03)	-0.04(0.04)	-0.03(0.03)

[1]. G^I_{i-j} = direct-maternal differences between lines i and j (see text for a complete explanation). [2] . SFA= C14:0+C15:0+C16:0+C17:0+C18:0. MUFA= C16:1+C18:1n-9+C18:1n-7. PUFA=C18:2n-6+C18:3n-3+C20:2n-6+C20:3n-6+C20:4n-6+C20:5n-3+C22:4n-6+C22:5n-3+C22:6n-3. n-3= C18:3n-3+C20:5n-3+C22:5n-3+C22:6n-3. n-6= C18:2n-6+C20:2n-6+C20:3n-6+C20:4n-6+C22:4n-6. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 18. Direct-maternal effect differences between lines[1] (standard error) for SFA and MUFA composition (mg/ 100 g muscle) of the *Longissimus* muscle.

Trait[2]	[1] G^I_{A-H}	G^I_{A-L}	G^I_{A-V}	G^I_{H-V}	G^I_{L-H}	G^I_{L-V}
C14:0	2.7(2.9)	1.6(2.3)	5.0(2.3)*	2.3(2.3)	1.0(2.9)	3.3(2.3)
C15:0	0.6(0.5)	0.5(0.4)	0.8(0.4)*	0.1(0.4)	0.1(0.5)	0.3(0.4)
C16:0	28(25)	22(20)	37(20)	9(20)	6(25)	15(20)
C16:1	6.9(5.2)	4.1(4.1)	8.2(4.1)*	1.3(4.1)	2.7(5.2)	4.1(4.1)
C17:0	0.8(0.6)	0.6(0.5)	0.9(0.5)	0.1(0.5)	0.2(0.6)	0.3(0.5)
C18:0	6.2(5.2)	5.1(4.1)	8.6(4.1)*	2.3(4.1)	1.1(5.2)	3.4(4.1)
C18:1 n-7	1.3(1.3)	1.2(1.0)	1.9(1.0)	0.6(1.0)	0.1(1.3)	0.7(1.0)
C18:1 n-9	46(30)	28(24)	50(24)*	3(24)	17(30)	21(24)

[1]. G^I_{i-j} = direct-maternal differences between lines i and j (see text for a complete explanation). [2]. C14:0 = myristic acid C15:0 = pentadecanoic acid C16:0 = palmitic acid C16:1 = palmitoleic acid C17:0 = heptadecanoic acid C18:0 = stearic acid C18:1 n-7 = vaccenic acid C18:1 n-9 = oleic acid. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 19. Direct-maternal effect differences between lines[1] (standard error) for PUFA composition (mg/ 100 g muscle) of the *Longissimus* muscle.

Trait[2]	[1] G^I_{A-H}	G^I_{A-L}	G^I_{A-V}	G^I_{H-V}	G^I_{L-H}	G^I_{L-V}
C18:2 n-6	30(20)	24(16)	32(16)*	1(16)	6(20)	7(16)
C18:3 n-3	4.0(2.5)	2.8(1.9)	3.9(1.9)*	-0.1(1.9)	1.2(2.5)	1.1(1.9)
C20:2 n-6	0.2(0.3)	0.3(0.2)	0.3(0.2)	0.0(0.2)	-0.1(0.2)	0(0.2)
C20:3 n-6	0.1(0.2)	-0.1(0.2)	0.1(0.2)	0.0(0.2)	0.2(0.2)	0.2(0.2)
C20:4 n-6	0.4(1.3)	0.3(1.0)	-0.1(1.0)	-0.4(1.0)	0.7(1.3)	-0.2(1.0)
C20:5 n-3	-0.7(0.6)	-0.5(0.5)	-0.2(0.5)	0.4(0.5)	-0.1(0.6)	0.3(0.5)
C22:4 n-6	-0.1(0.3)	-0.2(0.2)	-0.2(0.2)	-0.1(0.2)	0.1(0.3)	-0.1(0.2)
C22:5 n-3	0.4(0.5)	0.3(0.4)	0.1(0.4)	-0.3(0.4)	0.0(0.5)	-0.2(0.4)
C22:6 n-3	-1.1(1.6)	0.2(1.3)	0.4(1.3)	1.6(1.3)	-1.4(1.6)	0.2(1.3)

[1]. G^I_{i-j} = direct-maternal differences between lines i and j (see text for a complete explanation). [2]. C18:2 n-6 = linoleic acid C18:3, n-3 = linolenic acid, C20:2 n-6 = eicosadienoic acid, C20:3 n-6 = eicosatrienoic acid, C20:4 n-6 = arachidonic acid, C20:5 n-3 = eicosapentanoic acid, C22:4 n-6 = docosatetraenoic acid, C22:5 n-3 = docosapentanoic acid, C22:6 n-3 = docosahexanoic acid. *$P < 0.05$ (significant difference at $\alpha = 0.05$).

6.4.4 Grand-maternal effects.

Differences for the grand-maternal effect between lines are shown in Tables 20, 21, 22 and 23. As discussed in Chapters 2 and 3, the standard errors of the corresponding contrasts for direct-maternal effects (Tables 16, 17, 18 and 19) were higher than those for grand-maternal effects, showing that our data structure was better suited to estimate grand-maternal effects than direct-maternal effects. In contrast to direct-maternal effects, no significant contrasts were found for grand maternal effects, clearly indicating that the importance of the latter should be lower than the importance of the former.

Table 20. [1]Grand-maternal effect differences between lines (standard error) for pH, colour, intramuscular fat (IMF, g/100g muscle) and protein (g/100g muscle) of the *Longissimus* muscle.

Trait[2]	[1] $G^{M'}_{A-H}$	$G^{M'}_{A-L}$	$G^{M'}_{A-V}$	$G^{M'}_{H-V}$	$G^{M'}_{L-H}$	$G^{M'}_{L-V}$
pH	0.03(0.02)	0.01(0.02)	0.02(0.02)	-0.02(0.02)	0.02(0.02)	0.00(0.02)
L*	-0.99(0.88)	-0.59(1.10)	-0.44(1.16)	0.55(0.88)	-0.40(0.88)	0.15(1.02)
a*	-0.05(0.39)	-0.35(0.44)	-0.42(0.51)	-0.37(0.39)	0.31(0.39)	-0.06(0.45)
b*	-0.48(0.33)	-0.27(0.38)	-0.74(0.44)	-0.26(0.33)	-0.21(0.33)	-0.47(0.39)
IMF	-0.02(0.07)	-0.10(0.08)	-0.11(0.09)	-0.09(0.07)	-0.09(0.07)	0.00(0.08)
Protein	0.08(0.12)	0.05(0.14)	-0.17(0.16)	-0.09(0.12)	0.03(0.12)	-0.12(0.14)

[1]. $G^{M'}_{i-j}$ = grand-maternal differences between lines i and j (see text for a more complete explanation). [2]. L*= lightness of the *longissimus* muscle.

a*= redness of the *longissimus* muscle. b*= yellowness of the *longissimus* muscle.

Table 21. [1]Grand-maternal effect differences between lines (standard error) for fatty acid groups (mg/100 g muscle) and fatty acid ratios of the *Longissimus* muscle.

Trait[2]	[1] $G^{M'}_{A-H}$	$G^{M'}_{A-L}$	$G^{M'}_{A-V}$	$G^{M'}_{H-V}$	$G^{M'}_{L-H}$	$G^{M'}_{L-V}$
SFA	-5(20)	-34(23)	-30(26)	-25(20)	28(20)	2(23)
MUFA	-1(20)	-35(23)	-32(26)	-30(20)	34(20)	3(23)
PUFA	-1(11)	-17(12)	-17(14)	-16(11)	16(11)	0(12)
n-3 PUFA	0.0(1.0)	-1.5(1.1)	-1.2(1.2)	-1.3(1.0)	1.5(1.0)	0.2(1.1)
n-6 PUFA	4(10)	-10(12)	-11(14)	-15(10)	15(10)	0(12)
n-6/n-3	0.07(0.15)	-0.19(0.17)	-0.13(0.19)	-0.20(0.15)	0.03(0.15)	0.05(0.17)
PUFA/SFA	0.03(0.02)	0.04(0.03)	0.03(0.03)	0.00(0.02)	-0.01(0.02)	0.00(0.03)

[1]. $G^{M'}_{i-j}$ = grand-maternal differences between lines i and j (see text for a more complete explanation). [2].SFA= 14:0+C15:0+C16:0+C17:0+C18:0. MUFA= C16:1+C18:1n-9+C18:1n-7. PUFA=C18:2n-6+C18:3n-3+C20:2n-6+C20:3n-6+C20:4n-6+C20:5n-3+C22:4n-6+C22:5n-3+C22:6n-3. n-3= C18:3n-3+C20:5n-3+C22:5n-3+C22:6n-3. n-6= C18:2n-6+C20:2n-6+C20:3n-6+C20:4n-6+C22:4n-6.

Table 22. [1]Grand-maternal effect differences between lines (standard error) for SFA and MUFA composition (mg/ 100 g muscle) of the *Longissimus* muscle.

Trait[2]	[1] $G^{M'}_{A-H}$	$G^{M'}_{A-L}$	$G^{M'}_{A-V}$	$G^{M'}_{H-V}$	$G^{M'}_{L-H}$	$G^{M'}_{L-V}$
C14:0	-0.1(1.6)	-2.1(1.8)	-2.6(2.1)	-2.5(1.6)	2.1(1.6)	-0.4(1.8)
C15:0	0.0(0.3)	-0.4(0.3)	-0.4(0.3)	-0.4(0.3)	0.4(0.3)	0.0(0.3)
C16:0	-6(13)	-19(15)	-18(17)	-12(13)	12(13)	1(15)
C16:1	-1.0(2.8)	-5.1(3.2)	-4.7(3.7)	-3.7(2.8)	4.1(2.8)	0.4(3.2)
C17:0	0.0(0.3)	-0.4(0.4)	-0.5(0.5)	-0.5(0.3)	0.4(0.3)	-0.1(0.4)
C18:0	-0.1(2.9)	-4.4(3.3)	-4.8(3.7)	-4.6(2.9)	4.2(2.9)	-0.4(3.3)
C18:1 n-7	0.1(0.7)	-1.0(0.8)	-1.1(0.9)	-1.1(0.7)	1.1(0.7)	0.0(0.8)
C18:1 n-9	-1(16)	-28(18)	-26(21)	-25(16)	27(16)	2(18)

[1]. $G^{M'}_{i-j}$ = grand-maternal differences between lines i and j (see text for a more complete explanation). [2]. C14:0 = myristic acid, C15:0 = pentadecanoic, acid C16:0 = palmitic acid, C16:1 = palmitoleic acid, C17:0 = heptadecanoic acid, C18:0 = stearic acid, C18:1 n-7 = vaccenic acid, C18:1 n-9 = oleic.

Table 23. [1]Grand-maternal effect differences between lines (standard error) for PUFA composition (mg/ 100 g muscle) of the *Longissimus* muscle.

Trait[2]	[1] $G^{M'}_{A-H}$	$G^{M'}_{A-L}$	$G^{M'}_{A-V}$	$G^{M'}_{H-V}$	$G^{M'}_{L-H}$	$G^{M'}_{L-V}$
C18:2 n-6	4(11)	-13(12)	-13(14)	-17(11)	17(11)	0(12)
C18:3 n-3	0.2(1.3)	-1.8(1.5)	-1.6(1.7)	1.8(1.3)	2.1(1.3)	0.2(1.5)
C20:2 n-6	0.05(0.10)	-0.05(0.10)	-0.01(0.10)	-0.14(0.10)	0.10(0.10)	0.00(0.10)
C20:3 n-6	0.10(0.10)	-0.01(0.12)	0.02(0.14)	-0.08(0.10)	0.12(0.10)	0.04(0.12)
C20:4 n-6	0.17(0.73)	0.31(0.83)	-0.17(0.96)	-0.34(0.73)	-0.14(0.73)	-0.48(0.83)
C20:5 n-3	-0.19(0.33)	-0.09(0.38)	-0.13(0.44)	0.06(0.33)	-0.10(0.33)	-0.04(0.38)
C22:4 n-6	0.01(0.12)	0.04(0.14)	0.03(0.16)	0.02(0.12)	0.03(0.12)	-0.01(0.14)
C22:5 n-3	-0.28(0.25)	0.03(0.28)	-0.20(0.32)	0.08(0.25)	-0.31(0.25)	-0.23(0.28)
C22:6 n-3	-0.5(0.9)	0.5(1.0)	-0.8(1.2)	-0.2(0.9)	-1.1(0.9)	-1.3(1.0)

[1]. $G^{M'}_{i-j}$ = grand-maternal differences between lines i and j (see text for a more complete explanation). [2].C18:2 n-6 = linoleic acid, C18:3 n-3 = linolenic acid, C20:2 n-6 = eicosadienoic acid, C20:3 n-6 = eicosatrienoic acid, C20:4 n-6 = arachidonic acid, C20:5 n-3 = eicosapentanoic acid, C22:4 n-6 = docosatetraenoic acid, C22:5 n-3 = docosapentanoic acid, C22:6 n-3 = docosahexanoic acid.

6.4.5 Maternal heterosis.

Estimates of maternal heterosis effects are shown in Tables 24, 25, 26 and 27. No significant differences were found. Many results of positive heterosis, regarding litter size, have been reported (Brun and Saleil, 1994; Khalil and Afifi, 2000; Baselga et al. 2003; Brun and Baselga, 2005; Youssef et al., 2008). In Chapters 2 and 3 it was reported that maternal heterosis estimates were significantly negative for the majority of growth and carcass traits in crosses involving lines with high prolificacy (H and LP lines). However, our results did not confirm this negative heterosis trend for meat quality traits, perhaps because these traits are less dependent on litter size than growth and carcass traits. Performing the analysis with the covariate number born alive included into the models, all regression coefficients were not significant and the estimates of the maternal heterosis were roughly the same that when the covariate was not considered. Also, Sellier (1988) indicated that heterosis, in general, for quality of pork does not exist in most breed crosses.

Table 24. [1]Maternal heterosis (standard error) for pH, colour, intramuscular fat (IMF, g/100g muscle) and protein (g/100g muscle) of the *Longissimus* muscle.

Trait[2]	[1] H_{AH}^{M}	H_{AL}^{M}	H_{AV}^{M}	H_{HV}^{M}	H_{LH}^{M}	H_{LV}^{M}
pH	0.00(0.02)	0.00(0.02)	-0.01(0.02)	0.01(0.02)	0.01(0.02)	0.04(0.02)
L*	-0.44(0.87)	-0.86(1.02)	-0.12(0.87)	-0.92(0.72)	-0.37(0.72)	-0.74(0.72)
a*	-0.10(0.38)	0.16(0.44)	-0.09(0.38)	0.39(0.32)	0.00(0.32)	-0.08(0.32)
b*	-0.29(0.33)	-0.38(0.38)	-0.06(33)	-0.26(0.27)	-0.23(0.27)	-0.21(0.27)
IMF	-0.11(0.07)	-0.02(0.07)	0.02(0.07)	0.02(0.05)	0.03(0.05)	0.01(0.05)
Protein	0.02(0.12)	-0.18(0.14)	-0.08(0.12)	-0.05(0.10)	-0.04(0.10)	-0.12(0.10)

[1]. H_{ij}^{M} = maternal heterosis between lines i and j. [2] . L*= lightness of the *longissimus* muscle. a*= redness of the *longissimus* muscle. b*= yellowness of the *longissimus* muscle.

Table 25. [1]Maternal heterosis (standard error) for fatty acid groups (mg/100 g muscle) and fatty acid ratios of the *Longissimus* muscle.

Trait[2]	[1] H_{AH}^{M}	H_{AL}^{M}	H_{AV}^{M}	H_{HV}^{M}	H_{LH}^{M}	H_{LV}^{M}
SFA	-32(20)	0(23)	9(20)	2(17)	4(17)	0(17)
MUFA	-30(20)	0(23)	12(19)	3(16)	5(16)	-1(16)
PUFA	-15(11)	-2(12)	4(11)	1(9)	3(9)	0(9)
n-3 PUFA	1.2(1.0)	0.2(1.1)	0.4(1.0)	0.4(0.8)	0.4(0.8)	0.3(0.8)
n-6 PUFA	-7(10)	7(12)	7(10)	-2(9)	-1(9)	1(9)
n-6/n-3	-0.09(0.14)	0.04(0.17)	0.06(0.14)	-0.05(0.12)	-0.04(0.12)	-0.12(0.12)
PUFA/SFA	0.03(0.02)	0.00(0.02)	0.00(0.02)	-0.01(0.02)	0.00(0.02)	0.00(0.02)

[1]. H_{ij}^{M} = maternal heterosis between lines i and j. [2] .SFA= C14:0+C15:0+C16:0+C17:0+C18:0. MUFA= C16:1+C18:1n-9+C18:1n-7. PUFA=C18:2n-6+C18:3n-3+C20:2n-6+C20:3n-6+C20:4n-6+C20:5n-3+C22:4n-6+C22:5n-3+C22:6n-3. n-3= C18:3n-3+C20:5n-3+C22:5n-3+C22:6n-3. n-6= C18:2n-6+C20:2n-6+C20:3n-6+C20:4n-6+C22:4n-6.

Table 26. [1]Maternal heterosis (standard error) for SFA and MUFA composition (mg/100 g muscle) of the *Longissimus* muscle.

Trait[2]	[1] H_{AH}^{M}	H_{AL}^{M}	H_{AV}^{M}	H_{HV}^{M}	H_{LH}^{M}	H_{LV}^{M}
C14:0	-2.7(1.6)	-1.0(1.8)	0.1(1.6)	-0.3(1.3)	0.5(1.3)	-0.2(1.3)
C15:0	-0.37(0.3)	-0.03(0.3)	0.14(0.3)	0.04(0.3)	0.08(0.3)	0.01(0.3)
C16:0	-21(13)	5(15)	8(13)	1(11)	3(11)	3(11)
C16:1	-4(3)	0(3)	2(3)	1(2)	1(2)	1(2)
C17:0	-0.43(0.35)	0.08(0.40)	0.16(0.35)	-0.11(0.29)	-0.03(0.29)	-0.07(0.29)
C18:0	-4.1(2.8)	-0.9(3.3)	1.4(2.8)	0.2(2.3)	0.8(2.3)	-0.1(2.3)
C18:1 n-7	-0.96(0.7)	-0.17(0.8)	0.39(0.7)	0.05(0.6)	0.29(0.6)	0.10(0.6)
C18:1 n-9	-25(16)	0(18)	9(16)	2(13)	3(13)	-1(13)

[1]. H_{ij}^{M} = maternal heterosis between lines i and j. [2]. C14:0 = myristic acid, C15:0 = pentadecanoic acid, C16:0 = palmitic acid, C16:1 = palmitoleic acid, C17:0 = heptadecanoic acid, C18:0 = stearic acid, C18:1 n-7 = vaccenic acid, C18:1 n-9 = oleic acid.

Table 27. [1]Maternal heterosis (standard error) for PUFA composition (mg/100 g muscle) of the *Longissimus* muscle.

Trait[2]	[1] H_{AH}^{M}	H_{AL}^{M}	H_{AV}^{M}	H_{HV}^{M}	H_{LH}^{M}	H_{LV}^{M}
C18:2 n-6	-11(11)	7(13)	6(11)	-2(9)	0(9)	1(9)
C18:3 n-3	-1.4(1.3)	1.0(1.5)	1.1(1.3)	-0.2(1.1)	0.1(1.1)	0.2(1.1)
C20:2 n-6	-0.10(0.10)	0.10(0.12)	0.03(0.10)	-0.03(0.09)	0(0.09)	0.10(0.09)
C20:3 n-6	0.02(0.10)	0.03(0.12)	0.06(0.10)	-0.16(0.9)	-0.12(0.09)	-0.07(0.09)
C20:4 n-6	-0.8(0.73)	-0.80(0.84)	-1.23(0.73)	0.81(0.60)	0.21(0.60)	-0.08(0.60)
C20:5 n-3	0.16(0.33)	-0.23(0.39)	0.07(0.33)	-0.30(0.28)	-0.08(0.28)	0.13(0.28)
C22:4 n-6	0.04(0.12)	-0.08(0.14)	0.03(0.12)	-0.05(0.10)	-0.08(0.10)	-0.11(0.10)
C22:5 n-3	-0.39(0.25)	-0.34(0.28)	-0.19(0.25)	0.40(0.21)	0.03(0.21)	0.29(0.21)
C22:6 n-3	-1.1(0.9)	-1.9(1.1)	-1.7(0.9)	0.3(0.7)	-0.1(0.7)	0.0(0.7)

[1]. H_{ij}^{M} = maternal heterosis between lines i and j. [2]. C18:2 n-6 = linoleic acid, C18:3 n-3 = linolenic acid, C20:2 n-6 = eicosadienoic acid, C20:3 n-6 = eicosatrienoic acid, C20:4 n-6 = arachidonic acid, C20:5 n-3 = eicosapentanoic acid, C22:4 n-6 = docosatetraenoic acid, C22:5 n-3 = docosapentanoic acid, C22:6 n-3 = docosahexanoic acid.

6.5 CONCLUSIONS.

Significant differences regarding both direct-maternal effects and differences between purebred lines have been found between A and V lines for SFA, MUFA, PUFA, n-3 PUFA, n-6 PUFA. Overall, for the majority of individual fatty acids, meat from the A line was the fattiest. No significant differences were found for contrasts involving other lines and the A line, but there were indications that the A line had the highest contents of different groups of fatty acids. Regarding the comparisons between the crosses to the V line, the crossbred AH was superior for IMF, SFA, MUFA, PUFA, n-3 PUFA, n-6 PUFA and for certain individual fatty acids. Again, the results show that those contrasts involving the A line showed positive values (the fattiest results), and probably those involving the line V showed negative values (the leanest results). However, no significant differences were found for the contrasts All?-V, which is an indication of the lack of an overall heterotic effects. In general, the reciprocal cross effects were not significant. 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 effects to those obtained in the comparison between lines and crosses were obtained for the direct-maternal effects. No significant differences were found for the grand-maternal effects, and in general were of lower magnitude than the direct-maternal effects. No significant values of maternal heterosis were found and were explained by the relative independence of meat quality traits from litter size.

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7 GENERAL DISCUSSION

At present, meat production in rabbits is usually based on a three-way crossbreeding scheme (Baselga, 2004) that needs maternal and paternal lines.The first cross is between two maternal lines for the production of the crossbred female, which is used as doe stock on commercial farms. These females are expected to show better reproductive performance than the average of the lines involved in the cross, due to the advantage of heterosis and complementarity in reproductive traits (Ragab, 2012).The second cross consists of mating these crossbred does to males from a paternal line in order to produce the more superior rabbits to slaughter.

Paternal lines are usually selected for post-weaning daily gain or some weight close to slaughter time (Piles et al., 2004) or related to carcass composition (Nagy et al., 2006) but recently appeared new criteria of selection, for example residual feed consumption (Larzul and Rochambeau, 2005) and post-weaning growth under food restriction (Garreau et al., 2008).

The direct criteria used in selection programs of maternal lines are commonly related with reproductive traits as number weaned or number born alive per litter (Baselga and García, 2002). Also, selection for ovulation rate and uterine capacity has been successfully performed as indirect ways for improving prenatal survival and litter size in rabbits (Ibañez et al., 2004), and other objectives related with the capability of the

does to attend the litter during the lactation and individual weight has been considered (Garreau et al., 2004).

Since the late 70s, at the farms of the Animal Science Department of the Polytechnic University of Valencia (UPV, Spain) research has been undertaken involving a rabbit breeding program to develop genetic material of interest for meat rabbit production under a three-way breeding scheme. The UPV has established a network of selection-multiplication centres from which the lines are made available to commercial farms at low cost (Baselga, 2004). The UPV program has included the development of a paternal line (line R) and four maternal lines (lines A, V, H and LP). All criteria used to select maternal and paternal lines have a clear economic importance (Armero and Blasco, 1992; Cartuche et al., 2013). In this sense, growth characteristics and reproductive performance traits are those considered in paternal and maternal lines, respectively. Although these maternal lines are not selected for growth characteristics, it is obsvious that these are relevant traits, because crossbred does from these maternal lines provide to the rabbits for slaughter 50% of their genes. Thus, the overall objective of this thesis was to deaply characterize growth performance and carcasses and meat characteristic from the different genetic types (purebreds and crossbreds) derived from the four maternal lines involved in the UPV, aforementioned, rabbit breeding program.

Using the complete data set and pedigree of the lines from their foundation (Chapter 1), the comparison between them for weight at weaning (WW, 28 days), slaughter weight (SW, 63 days) and average daily gain between weaning and slaughter (ADG) at their foundation was carried out. Also, a comparison of these lines at fixed times, allowed us to observe how these traits are affected by selection for reproductive traits across generations. With regard to contrast at foundation the line A was superior to V line, with a probability of this contrast to be greater than 0 of 0.99, 0.97 and 0.75 for

WW, SW and ADG, respectively. Also at foundation the lines H and LP were heavier than V and A lines. The procedures for the creation of A and V lines were from NZW and from maternal lines, respectively, while the H and LP were apparently created from crossbred does obtained from meat rabbit commercial populations, that could have some introgression of genes of paternal lines that would explain the superiority of H and LP lines for growth traits.

Cifre et al. (1998) compared the H line at foundation with the contemporary generation of the V line and they found that the H line was always significantly heavier than the V line for WW, and had also a higher SW, although the ADG was not significantly different, it must be noted that in this case the interaction line-year-season was not fitted into the model.

Getting differences at foundation of largely selected populations relies in one hand on mixed model estimations and predictions, but more importantly on keeping the selected populations sharing the same environment for the whole selection process. This is a task difficult to be achieved in most of the livestock selected populations, and we are only aware of equivalent estimations by Ragab and Baselga (2011), regarding reproductive traits, using the same lines.

For the contrasts between lines after a number of generations of selection, two periods were considered; the most recent periods when different sets of three of the lines were housed together at the nucleus, having the same type of cages and management. They were from March 1997 to August 1998 (period 1) for lines A, V and H, and from December 2009 to November 2010 (period 2) for lines A, V and LP. In these analyses the line effects from a fixed model without additive genetic effects refers to the real genetic merit of the lines at the time of comparison, being consequence of differences at foundation, selection and genetic drift. The observed differences at the two different

times of the process of selection follow the same trend than the differences estimated at the origin of lines but their magnitude decrease. The lines differ in the number of generations of selection and this factor could explain part of the decrease as a correlated response (positive genetic correlation between NW and growth traits: 0.29, 0.13 and 0.15, respectively, for WW, SW and ADG) and for the effect of a concomitant, non-programmed selection tending to partly benefit the selection of animals with more weight, mainly in the V line. From the complete data set and the model including additive genetic effects it can be possible to compute expected differences between the lines at fixed times using the complete model and data set, as the contrast between lines during the times shared (period 1 and period 2), plus the difference between the averages of the additive genetic values of the animals of each line having data in this period. The expected differences between lines were similar to the observed differences. This similarity possibly indicates the appropriateness of the models used to analyse the traits. Once again, we are not aware of a similar approach previously reported for internal validation of genetic evaluation models.

In addition to the characterization of the lines based on purebred historical data, newly generated information from the diallel cross involving the four aforementioned lines was used to obtain records on rabbits mothered by females from crosses and purebred animals in the diallel cross, having as sires, bucks from R line, selected for daily growth. This is highly valuable information to the rabbit production sector given that the usual production schema is a three-ways cross. Chapters 2, 3 and 4 had the objective of evaluating the value of the maternal lines to determine the growth, feed use, carcass and meat characteristics of their three-way crossbred progeny.

The rabbits of the four maternal lines and the twelve simple crosses, corresponding to the type of does of the diallel cross, were distributed in four Spanish farms. The V

line was present on all farms in order to connect records among them and to be used as reference group. Together with the V line, lines A and LP were located in Valencia, the H line was housed in Sant Carles de la Rápita (Tarragona), and the 12 single crosses were distributed between Altura (Castellón) and Rioseco de Tapia (León). A set of six single crosses in Altura, and another set of six, that are the reciprocal of the first set, in Rioseco. However, because the V line was the only genetic type across all the farms no interaction between farm and genetic type could be considered.

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). Thus, five different types of genetic parameters were present: direct additive genetic effects, maternal additive genetic effects, grand-maternal genetic effects, individual heterosis and maternal heterosis. These genetic parameters cannot be estimated individually, however, direct and maternal genetic effects, and individual heterosis were combined into one parameter and functions of them were estimated.

In Chapter 2, genetic group differences and crossbreeding parameters for body weight at weaning (28 days, $\mathbf{BW_{28}}$), body weight at slaughter (at 63 days, $\mathbf{BW_{63}}$), post-weaning average daily gain (**ADG**), cage feed intake (**FI**) and cage feed conversion ratio (**FCR**) were measured in rabbits from the above described experimental trial. Young rabbits were controlled during the complete fattening period and the traits were recorded weekly, being the cage the experimental unit for FI and FCR. The whole of the fattening period lasted five weeks. The intervals studied were three: the two first weeks of fattening (the most critical weeks for the survival of young rabbits (Rashwan and Marai, 2000)), the following three weeks (to finish the fattening period) and the whole

of the five fattening weeks. The date of any death of young rabbit was recorded to adjust the FI in every week.

Mean values for growth traits were within the range of commercial weight in Spain (MAGRAMA, 2012). Few significant differences between lines, crosses and V line, and reciprocal crosses between them have been observed. For purebred and crosses, the differences in favor of the line A (or the crosses involving A line) for BW_{28} could be related with litter size at weaning, because this line has the lowest number of born alive and the lowest number of weaned (Ragab and Baselga, 2011). For A and V lines, we obtained similar results for BW_{28} as Feki et al. (1996). The differences in favor of line A for BW_{28} disappeared along fattening period, probably due to compensatory growth (Testik et al., 1999). Thus, for BW_{63}, no significant differences were observed between the crossbred groups. Negative values of maternal heterosis observed in this study could be related to the effects of prolificacy on growth, but results obtained using number born alive as a covariate did not support this hypothesis.

With regard to BW_{28}, BW_{63} and ADG, differences between purebred types, as well as differences between direct genetic-maternal effects could be compared to the observed current differences between lines obtained in Chapter 1. When both results are compared very similar results are observed for ADG, in spite that in Chapter 1 purebred animals are considered, while three-ways or two-way crossbred animals were used in Chapter 2. In addition, Chapter 1 considered records from a single farm while Chapter 2 analyzed data from 4 different farms, only connected by the V line.

In Chapter 3, the genetic group effects and the crossbreeding genetic parameters of slaughter and carcass traits were estimated. The slaughter traits were recorded in a commercial slaughterhouse for animals from Altura and in the experimental

slaughterhouse of the Animal Science Department of the UPV for the rest of the animals. The slaughter traits recorded were live weight at 63 days (day of slaughter), commercial skin weight, full gastrointestinal tract weight, hot carcass weight, and dressing percentage. After slaughtering, the carcasses were stored at 4º C during 24 hours. The carcass traits studied were carcass colour, commercial carcass weight, head weight, liver weight, kidneys weight, thoracic viscera weight, reference carcasses weight, scapular carcass weight, perirenal fat weight, hind leg weight, loin weight, fore leg weight, thoracic cage weight and meat bone ratio. These traits were recorded in the meat laboratory of the Department of Animal Science of the UPV following the official criteria and terminology of the World Rabbit Scientific Association (Blasco et al., 1993). The averages values for all the traits were within the range in the bibliography consulted (Gómez et al., 1998; Hernández et al., 2006). The A and LP lines had the lowest values for dressing percentage (-1.71 and -1.98 compared with H line and -1.49 and -1.75 with the V line, respectively). The A line was the heaviest for commercial carcass weight (83 g. compared with the line H and 60 g. with the V line). The differences in lines regarding dressing percentage were transferred to the crossbred groups involving those lines although the magnitude of them was lower. For the rest of traits, no relevant differences were observed between the crossbred groups and between reciprocal crosses.

Grand-maternal effects were of lower magnitude and of opposite sign than the direct-maternal effects. Afifi et al. (1994), Piles et al. (2004), Ouyed et al. (2008) and Al-Saef et al. (2009) reported that these effects were not significant for the traits measured in our study.

The estimates of maternal heterosis were, in general, negative, and this results, as commented before for the growth traits could be consequence of positive heterotic

effects on litter size, but, as commented for Chapter 2, the results obtained using number born alive as a covariate did not support this hypothesis. In some studies that litter size was introduced in the model, the values of heterosis were low, positives or zero as for example Piles et al. (2004) did not obtain significant heterosis in a crossbreeding experiment, Ouyed et al. (2011) generally obtained zero or low heterosis for body conformation and carcass traits and Al-Saef et al. (2009) obtained that the heterosis estimates were mostly positive but only significant for CSkW, HW and LHW.

In Chapter 4, meat quality traits were measured. These traits were pH, colour, intramuscular fat (IMF), protein, fatty acid groups (SFA, MUFA, PUFA, n-3PUFA and n-6PUFA), fatty acid ratios (n-6/n-3 and PUFA/SFA) and individual fatty acid profiles. pH and meat colour were measured in 950 *Longissimus* muscles (LM) which were excised from carcass used in Chapter 3. The rest of the meat quality traits were recorded by NIRS from a sample of 285 LM that were used before to measure pH, applying calibration equations previously developed (Zomeño et al., 2012). The averages values for all the traits were similar to those obtained in previous studies (Hernández and Gondret, 2006; Zomeño, 2013). In general no differences in pH and content protein were found. Hernández et al. (2006) studied pH differences between A and V lines and did not observe differences between them. The line A had significant differences with respect to V line for IMF, SFA, MUFA, PUFA, n-3PUFA and n-6PUFA of 0.23, 67, 66, 34, 3.1 and 25 (mg/100 g of muscle), respectively, and for the majority of individual fatty acids. Regarding the comparisons between the crosses and V line, the crossbred AH was superior content for IMF, SFA, MUFA, PUFA, n-3PUFA, n-6PUFA and for some of individual fatty acids. No significant differences were found for other contrasts but seems that the crossbreds involving A line had the higher content for IMF and fatty acids groups. No significant differences were found for the contrasts All-V, which is an

indication of the lack of overall heterotic effects. In general, the reciprocal cross effects were not significant.

Regarding crossbreeding parameters, there were significant differences between A and LP lines in direct-maternal effects for pH (0.08) and between A and V for IMF, SFA, MUFA, PUFA, n-3PUFA and n-6PuFA of 200, 63, 61, 33, 2.9 and 31 mg/100g, respectively, always in favor of the A line. No significant differences were found for grand-maternal effects, they were of lower magnitude than the direct-maternal effects. No significant values of maternal heterosis were found, if it is accepted that an important effect on the studied traits is mediated by the reproductive performance of the females, the lack of maternal heterosis could be explained by the relative independence of meat quality traits from litter size, as was reported in pigs by Sellier (1998).

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8 CONCLUSIONS

1- Important differences for growth traits were detected between maternal lines at their origin. These differences could be partly explained by their different foundation criteria.

2- These differences became smaller and less important after many generations of selection. This result could be a consequence of a correlated response on growth after the selection for litter size at weaning, as well as to direct response to a concomitant, non-programmed selection for growth traits, different in intensity between the lines, or also simply to be consequence of genetic drift, or some combination of these effects.

3- Strong agreement has been observed between the current observed differences of the lines and their expected values at defined periods of time. This result can be seen as an indicator of the appropriateness of the considered genetic models.

4- Few significant differences between lines, crosses and V line, and reciprocal crosses between them have been observed for growth, carcass and meat quality traits. 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.

5- The lack of significance can be a consequence of the relatively large standard errors and not necessarily due to an overall lack of effects. The extremes of 95%

confidence interval of the contrast effects could reach relevant values especially for dressing percentage.

6- Grand-maternal effects, in general, were of lower magnitude and of opposite sign than direct-maternal effects.

7- Negative values of maternal heterosis were observed, which can also be explained by the negative environmental effect that crossbred females provide to their offspring.

8- After making an overall view of the presented results, regarding growth, carcass and meat quality traits, the four maternal lines evaluated seem suitable for use in a three-way crossbreeding scheme, despite some differences between them.