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ANIMAL BREEDING AND REPRODUCTION BIOTECHNOLOGY



PRODUCTIVE CHARACTERISTICS OF FOUR MATERNAL LINES OF RABBIT

BY

Mohamed Mohamed Ragab

SUPERVISOR

Prof. Manuel Baselga Izquierdo

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TO

MY

Lovely Wife

Son Youssof

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ABSTRACT

The objective of this study was to compare litter size traits and kindling interval in four Spanish maternal lines of rabbit (A, V, H and LP lines) selected for litter size at weaning. The analysis were performed at the origin of the lines (data from June 1980 to February 2009) and during the last six year-seasons shared at the same farm by at least three lines (to analyze the A, V and H lines the data used were from December 2002 to May 2004 and to analyze the A, V and LP the data used were from September 2007 to February 2009).

The results can be summarized as follows:

- 1. Heritabilities estimated for litter size traits were generally low, being 0.14 for total born, 0.10 for number born alive, 0.08 for litter size at weaning (28 days), 0.08 for litter size at marketing (63 days) and 0.05 for kindling interval.
- 2. Direct genetic correlations between litter size at weaning and other traits were highly positive, being 0.80 with total born, 0.90 with number born alive and 0.96 with number marketed. However, the genetic correlation between litter size and kindling interval was negative (-0.24).
- 3. Low to moderate estimates for repeatability were observed for litter size traits, being 0.24 for total born, 0.20 for number born alive, 0.16 for number weaned, 0.15 for number marketed and 0.10 for kindling interval.
- 4. The inbreeding had a low negative effect on litter size traits. The effect on kindling interval was irrelevant.
- 5. At the origin, line V had a higher litter size (total, alive, weaned and marketed) than line A. Also, LP and H lines had higher litter sizes than the line A. In addition, LP line had higher litter size than line V. Regarding the kindling interval, line H had a shorter interval than line A, while line LP had a shorter interval than line V.
- 6. Analyzing the results of lines V, H and A from December 2002 to May 2004, lines H and V had a higher litter size than line A. Comparing lines V and H, the last line had the highest total born. However, the number of born alive was similar to line V, which showed higher litter size at weaning and litter size at marketing. Regarding the kindling interval, line V had shorter interval than lines A and H.
- 7. Analyzing the results of lines LP, V and A from September 2007 to February 2009, line V had a higher total born than line A. However, there were no differences between both lines in number born alive, litter size at marketing and kindling interval. Furthermore, no significant differences were found when comparing the LP line with lines V and A.

RESUMEN

El objetivo de este trabajo fue comparar el tamaño de camada y el intervalo entre partos en cuatro líneas maternales de conejo (A, V, H y LP) seleccionadas por tamaño de camada al destete. Los análisis se realizaron en el origen de las líneas (datos de junio 1980 a febrero de 2009) y en los últimos seis años-estación compartidos en la misma granja por al menos tres líneas (para analizar las líneas A, V y H se utilizaron los datos desde diciembre de 2002 hasta mayo de 2004 y para comparar las líneas A, V y LP se utilizaron los datos desde septiembre de 2007 hasta febrero de 2009.

Los resultados obtenidos fueron:

- 1. Las estimas de la heredabilidad para el tamaño de camada han sido bajas, siendo de 0,14 para el número de nacidos totales, 0,10 para el número de nacidos vivos, 0,08 para el tamaño de camada al destete (28 días), 0,08 para tamaño de camada al sacrificio (63 días) y 0,05 para el intervalo entre partos.
- 2. Las correlaciones genéticas entre el tamaño de camada al destete y los caracteres analizados son elevadas y positivas; 0,80 con el número de nacidos totales, 0,90 con el número nacidos vivos y 0,96 con el número de sacrificados. Sin embargo, la correlación genética entre el tamaño de camada al destete y el intervalo entre partos ha sido negativo (-0,24).
- 3. Las estimas de la repetibilidad han sido bajas-moderadas para los caracteres analizados; 0,24 para el número de nacidos totales, 0,20 para el número de nacidos vivos, 0,16 para el número de destetados, 0,15 para el número de sacrificados y 0,10 para el intervalo entre partos.
- 4. La consanguinidad ha tenido un pequeño efecto negativo sobre los caracteres del tamaño de camada. Su efecto positivo sobre el intervalo entre partos fue irrelevante.
- 5. Al analizar los resultados en el momento en el que se constituyen las líneas se observa que la Línea V tiene un mayor tamaño de camada (totales, vivos, destetados y sacrificados) que la línea A. También las líneas H y LP presentan mayores tamaños de camada que la línea A. Además, la línea LP presenta mayor tamaño de camada que la línea V. Al analizar el intervalo entre partos se observa que la línea H tiene un menor intervalo que la línea A, mientras que la línea LP tiene un menor intervalo que la línea V.
- 6. Al analizar los resultados de las líneas V, H y A desde diciembre de 2002 hasta mayo de 2004 se observa que las dos primeras líneas (V y H) presentan un mayor tamaño de camada que la línea A. Al comparar las líneas V y H se observa que el número de nacidos totales es mayor en la línea H. Sin embargo, el número de gazapos vivos es similar, siendo la línea V la que presenta mayor tamaño de camada al destete y número de sacrificados. Respecto al intervalo entre partos, la línea V presenta un menor intervalo que la línea A y H.
- 7. Al analizar los resultados de las líneas LP, V y A desde septiembre de 2007 hasta febrero de 2009 se observa que la línea V tiene un mayor número de nacidos totales que la línea A. Sin embargo, no existen diferencias entre ambas líneas en el número de nacidos vivos, el número destetados, el número de sacrificados y el intervalo entre partos. Además, no se han encontrado diferencias significativas al comparar la línea LP con las líneas V y A.

RESUM

L'objectiu d'aquest treball és comparar el nombre de llorigons així com l'interval entre parts en quatre línies maternals de conill (A, V, H i LP) seleccionades pel tamany de la ventrada al deslletament. Els anàlisis es van realitzar en dos moments; l'origen de cadascuna de les línies i en els últims sis anys-estació compartits en la mateixa granja per almenys tres línies: per a analitzar les línies A, V i H es van utilitzar les dades des de Desembre de 2002 fins a Maig de 2004 i per a comparar les línies A, V i LP es van utilitzar les dades des de Setembre de 2007 fins a Febrer de 2009.

Els resultats obtinguts han sigut els següents:

- 1 . Les estimes de l'heretabilitat per al tamany de la ventrada han sigut baixes; 0,14 per al nombre de nascuts totals, 0,10 per al nombre de nascuts vius, 0,08 per al tamany de la ventrada al deslletament (28 dies), 0,08 per al tamany de la ventrada al sacrifici (63 dies) i 0,05 per a l'interval entre parts.
- 2 . Les correlacions genètiques entre el tamany de la ventrada al deslletament i els caràcters analitzats van ser elevats i positius; 0,80 amb el nombre de nascuts totals, 0,90 amb el nombre nascuts vius i 0,96 amb el nombre de sacrificats. No obstant això, la correlació genètica entre el tamany de ventrada al deslletament i l'interval entre parts ha sigut negatiu (-0,24).
- 3 . Les estimes de la repetibilitat han sigut baixes-moderades per als caràcters analitzats; 0,24 per al nombre de nascuts totals, 0,20 per al nombre de nascuts vius, 0,16 per al nombre de deslletats, 0,15 per al nombre de sacrificats i 0,10 per a l'interval entre parts.
- 4 . La consanguinitat ha tingut un efecte negatiu sobre els caràcters del tamany de la ventrada i un efecte irrellevant sobre l'interval entre parts.
- 5 . Al analitzar els resultats en el moment en el qual es van constituir les línies s'observa que la Línia V té un major tamany de ventrada (totals, vius, deslletats i sacrificats) que la línia A. També les línies H i LP presenten majors tamanys de la ventrada que la línia A. A més, la línia LP presenta major tamany de la ventrada que la línia V. Al analitzar l'interval entre parts s'observa que la línia H té un menor interval que la línia A, mentre que la línia LP té un menor interval que la línia V.
- 6 . Al analitzar els resultats de les línies V, H i A des de Desembre de 2002 fins a Maig de 2004 s'observa que les dues primeres línies (V i H) presenten un major tamany de la ventrada que la línia A. Al comparar les línies V i H s'observa que el nombre de nascuts totals és major en la línia H. No obstant, el nombre de llorigons vius és similar, sent la línia V la que presenta major el tamany de la ventrada al deslletament i nombre de sacrificats. Respecte a l'interval entre part, la línia V presenta un menor interval que les línies A i H.
- 7 . Al analitzar els resultats de les línies LP, V i A des de Setembre de 2007 fins a Febrer de 2009 s'observa que la línia V té un major nombre de nascuts totals que la línia A. No obstant això, no existeixen diferències entre les línies en el nombre de nascuts vius, el nombre de sacrificats i l'interval entre parts. A més, no s'han trobat diferències significatives al comparar la línia LP amb les línies V i A.

RÉSUMÉ

L'objectif de ce travail est de comparer la taille de portée et l'intervalle entre misebas de quatre lignées des lapins (A, V, H et LP) sélectionnées pour la taille de portée au sevrage. Les analyses ont été réalisés en deux moments, l'origine de chacune de ces lignées et pendant les derniers six ferme-saison-années cohabitent au moins trois lignées: pour analyser les lignes A, V, et H, ils ont été utilisées des dates depuis décembre 2002 jusqu'a mai 2009 et pour comparer les lignées A, V, LP ils ont été utilisées des dates depuis décembre 2007 jusqu'a février 2009.

Les résultats obtenus ont été:

1. Les estimations de la heretabilité pour la taille de portée ont été faibles, de 0.14 pour le nombre de nés totaux, 0.10 pour le nombre de nés vivants, 0.08 pour la taille de portée a la sevrage (28 jours), 0.08 pour la taille de portée a la sacrifice (63 jours) et 0.05 pour l'intervalle entre mise-bas.

2. Les corrélations génétiques entre la taille de portée a la sevrage et les autres caractères analysés sont élevées et positives; 0.80 avec le nombre des nés totaux, 0.90 avec le nombre des nés vivants et 0.96 avec le nombre des sacrifiés, mais la corrélation génétique entre la taille de portée au sevrage et l'intervalle entre mise-bas a été négative.

3. Les estimations de la repetabilité ont été faibles- modérées pour les caractères analysés, 0.24 pour le caractère nombres des nés totaux, 0.20 pour le nombre de nés vivants, 0.16 pour le nombre de sevrés, 0.15 pour le nombre des sacrifiés et 0.10 pour l'intervalle entre mise-bas.

4. La consanguinité affecte négativement sur les caractères de la taille de portée et a un effet irrelevant sur l'intervalle entre mise-bas.

5. Analysant les résultats au moment de la constitution des lignées s'observe que la lignée V présente a taille de portée plus élevée (totaux, vivants, sevrés et sacrifiés) que la lignée A. Aussi les lignées H et LP présentent tailles de portées plus grandes que la lignée A. En plus la lignée LP présente taille de portée plus grande que la lignée V. Analysant l'intervalle entre mise-bas s'observe que la lignée H a une intervalle plus petit que la lignée A, alors que la lignée LP a un intervalle plus petit que la lignée V.

6. Analysant les résultats des lignées V, H et A depuis décembre 2002 jusqu'a mai 2004 s'observe que les de deux premières lignées (V et H) présentent une taille de portée plus grand que la lignée A. Si on compare les lignées V et H s'observe que les deux premières lignées (V et H) présentent une taille de portée plus grand que la lignée A. Comparant les lignées V et H s'observe que le nombre de nés totaux est plus grand a la lignée H; malgré que le nombre de lapereaux vivants est similaire, la lignée V c'est celle qui présente la plus grande taille de portée au sevrage et nombre de sacrifiés. Ce qui concerne l'intervalle entre mise-bas, la lignée V présente le plus faible intervalle.

7. Analysant les résultats des lignées LP, V et A depuis septembre 2007 jusqu'a février 2009 s'observe que la lignée V présente a nombre de nés totaux plus grand que la lignée A. Malgré, il n'existe pas des différences entre l'ensemble des lignées concernant le nombre de nés vivants, le nombre sèvres, nombre de sacrifiés et l'intervalle entre mise-bas. En plus, on n'a pas trouvés différences significatives comparant la lignée LP avec les lignées V et A.

RESUMO

O objetivo do trabalho foi comparar o tamanho de ninhada e o intervalo entre partos de quatro linhas maternas de coelhos (A, V, H e LP) selecionadas pelo tamanho de ninhada à desmama (TND).

As análises foram realizadas em dois momentos, no momento do origem de cada uma das linhas e nos últimos seis anos-estação com animais na mesma granja e com, ao menos, três linhas. Para analizar as linhas A, V e H utilizaram-se os dados de Dezembro de 2002 até Maio de 2004 e para comparar as linhas A, V e LP utilizaram-se os dados de Setembro de 2007 até Fevereiro de 2009.

Os resultados obtidos foram:

- 1. As estimações herdabilidades para o tamanho de ninhada foram baixas, sendo 0,14 para o número de nascidos totais, 0,10 para o número de nascidos vivos, 0,08 para o tamanho de ninhada à desmama (28 días), 0,08 para o tamanho de ninhada ao abate (63 días) e 0,05 para o intervalo entre partos.
- 2. As correlações genéticas entre o tamanho de ninhada à desmama (TND) e as caracteristicas analizadas foram altas e positivas; 0,80 entre TND e número de nascidos totais, 0.90 para TND e número nacidos vivos e 0,96 para TND e número de abatidos. A correlação genética entre TND e o intervalo entre partos foi negativa (-0,24).
- 3. A repetibilidade das características foram de baixas a moderadas para as características analizadas. Para número de nascidos totais foi de 0,24, para número de nascidos vivos foi 0,20, para número de destetados foi 0,16, para número de abatidos foi 0,15 e para el intervalo entre partos foi 0,10.
- 4. A consanguinidade teve efeito negativo sobre as características do tamanho de camada e efeito irrelevante sobre o intervalo entre partos.
- 5. Ao analizar os resultados no momento do origem das linhas verificou-se que a linha V teve maior tamanho de ninhada (totais, vivos, desmamados e abatidos) do que a linha A. As linhas H e LP também apresentaram maiores tamanhos de ninhada do que a linha A. A linha LP apresentó maior tamanho de ninhada do que a linha V. Para o intervalo entre partos, observa-se que a linha H teve um menor intervalo do que a linha A, enquanto que a linha LP teve um menor intervalo do que a linha V.
- 6. Ao analizar os resultados das linhas V, H e A desde Dezembro de 2002 até Maio de 2004, observou-se que as duas primeiras linhas (V e H) apresentaram maior tamanho de ninhada do que la línea A. Ao comparar as linhas V e H observou-se que o número de nascidos totais foi maior na linha H. Noentanto, o número de láparos vivos foi similar, sendo que a linha V é a que apresenta maior tamanho de ninhada à desmama e maior número de abatidos. Em relação ao intervalo entre parto, a linha V apresentou menor intervalo do que as linhas A e H.
- 7. Ao analizar os resultados das linhas LP, V e A desde Setembro de 2007 até Fevereiro de 2009, observou-se que a linha V apresentou maior número de nascidos totais do que a linha A. Entretanto, não foram detectadas diferenças entre ambas linhas no número de nascidos vivos, no número de desmamados, no número de abatidos e no intervalo entre partos. Também, no foram achadas diferenças significativas ao comparar a línea LP com as linhas V e A

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1. INTRODUCTION

1.1. RABBIT PRODUCTION

Now most of the rabbit meat production is in countries of the Mediterranean and in 2003 the world production of rabbits was 1 067 948 tonnes, with China the largest producer with 425 000 tonnes, followed by Italy with 222 000 tonnes and Spain with 115 000 tons, (FAO-STAT, 2003).

Rabbit, as a resource of animal meat, in efficient production systems, can turn 20 percent of the proteins they eat into edible meat. Comparable figures for other species are 22 to 23 percent for broiler chickens, 16 to 18 percent for pigs and 8 to 12 percent for beef so that with its fast production cycle might be an effective part of the solution for animal protein crisis, especially in the less developed countries (Lebas *et al.*, 1997).

Also, a similar calculation for the energy cost of these proteins is even more unfavourable to ruminants. When cattle or sheep are raised for meat production, most of the energy consumed by the herd or flock is used to maintain breeding females which have a low prolificacy: a maximum of 0.8 to 1.4 young per year against 40 for female rabbits because the female has a short period of pregnancy and a great ability to reproduce. So that the female rabbit can produce up to 80 kilograms of meat per year.

Even with the theoretical lower energy cost when cattle are raised for both milk and beef, rabbit meat is still more economical in terms of feed energy than beef. Rabbit meat production is therefore an attractive proposition, especially when the aim is to produce quality animal protein. Rabbits can also easily convert the available proteins in cellulose-rich plants, whereas it is not economical to feed these to chickens and turkeys - the only animals with higher energy and protein efficiency. The traditional grain and soycakes fed to these domestic poultry put them in direct competition with humans for food. For countries with no cereal surpluses, rabbit meat production is thus especially interesting.

1.2. Genetic improvement in rabbit

The objective of a genetic improvement program is the development and diffusion of genetic material to the farmers (Rochambeau, 1988). The organization of genetic improvement in rabbit is pyramid type, similar to the other prolific species like the pigs and poultry, the peak of the pyramid is the selection of especial lines (maternal and paternal lines) in the nucleus of selection. One nucleus of selection of rabbit can be enough for the replacement of 80 farms with an average of 400 does per farm (Ramón *et*

al., 1996), taking into account a replacement rate of 120% (Ramón and Rafel, 2002). The selection nuclei have to provide animals with a good sanitary condition, production capacity and genetic program (Torres *et al*, 1997).

The genetic improvement programmes that have to meet the needs of intensive production in rabbits are based on a three way crossbreeding scheme (Matheron and Rouvier, 1977; Rochambeau, 1988; Blasco, 1996 and Baselga 2004). A first cross involves two maternal lines generating the crossbred does, which are used as females for production in commercial farms. A second cross consists of mating these females to males of a paternal line to produce the rabbits to be slaughtered for meat. The paternal lines are selected to improve feed conversion rate, trait that is economically very important, but it is difficult and expensive to measure. So that, the criterion of selection is growth rate or weight at a given age because these traits are easy, not expensive to measure and have a negative genetic correlation with feed conversion rate (Blasco, 1984).

In this context, the development of maternal lines is a crucial activity of the companies and public institutions devoted to the genetic improvement of meat rabbit production. These lines are commonly selected for litter size traits, as litter size at birth or at weaning, following within line methods of selection. Crossbred does are expected to show better reproductive performance than purebred does. The cross between the maternal lines is to take advantage of the expected positive heterosis in reproductive traits, the eventual complementarity among the lines and the dissipation of the inbreeding accumulated within the lines (Baselga *et al.*, 2003). Because the usual methods of improving the lines are based on within-line selection, it is expected that the initial heterosis expressed in the cross will be maintained along the generations of selection and that the genetic progress obtained selecting the maternal lines will be capitalised on top of the heterosis and expressed in the crossbred does (Baselga *et al.*, 2003).

1.2.1. SELECTION OF MATERNAL LINES

The selection methods in maternal lines are more complicated than in sire lines (Baselga, 2004), because the males don't express themselves the litter size traits and the heritability of reproduction traits is so low than it is necessary to consider as many own and relative records as possible in genetic evaluation of the does and bucks. In addition, the generation interval is longer than in the case of the selection of sire lines and,

consequently, it could be necessary to take account some environmental and physiological effects into the models of evaluation (Armero *et al.*, 1995).

Reproductive capacity of does is one of the most important economic traits in meat production of rabbits (Sorensen *et al.*, 2001) so that a major objective of selection is to improve annual production per doe. Litter size at birth or at weaning have been main selection criteria in many selection experiments in rabbits (Rouvier, 1981; Estany *et al.*, 1989; García-Ximenez *et al.*, 1996; Gómez *et al.*, 1996; Brun *et al.*, 1998; El-Raffa *et al.*, 2000).

The advantage of selection for litter size at weaning compared with the number of live kits at birth is the indirect consideration of milk production and maternal ability of the does. The disadvantages are the lower heritability and the longer generation interval. Furthermore, in some cases, the selection criteria include litter size at birth and weight at a post weaning given time to prevent negative responses in adult weight (Bolet and Saleil, 2002a, b and c). Litter size at 63 days have economic relevance for the farmer but at this age the generation interval will be longer and the mortality of kits in this age more affected by environmental effects than by the genetic effects of the mother (Garcia *et al.*, 1982). So, it has been preferred to select for litter size at birth or weaning. There are other objectives for the selection of maternal lines like the number of teats (Rochambeau *et al.*, 1988) and there are proposals for including traits related with the ability of the doe to nourish the lactating progeny, such as weight at weaning (Garreau and Rochambeau, 2003), litter weight at weaning or total milk production (Khalil *et al.*, 2002; Garreau *et al.*, 2004; Abou Khadiga, 2008; Al-Saef *et al.*, 2008; Youssef *et al.*, 2008).

Other important reproductive traits that can be considered are the components of litter size as ovulation rate, foetal survival or uterine capacity. Selection for ovulation rate and uterine capacity have been analysed as indirect ways for improving prenatal survival and litter size in rabbits (Ibáñez-Escriche *et al.*, 2004, 2006; Blasco *et al.*, 2005; Mocé *et al.*, 2005; Santacreu *et al.*, 2005). Rabbit birth weight presents a great variability within each litter (Bolet *et al.*, 1996, 2007) and reducing this heterogeneity might be useful in selection programs since it induces a high mortality as a result of losses in the weakest rabbits. Selection for hyperprolificacy in maternal lines was a successful way to improve litter size in rabbits (Cifre *et al.*, 1998). Longevity of females has been introduced recently in rabbit selection programs (Sánchez *et al.*, 2004, 2008), although it is difficult to improve through conventional breeding methods because of

the low heritability, the time needed to obtain information and the presence of censored data. Sánchez *et al.* (2004) concluded that both longevity and litter size are not antagonistic objectives in breeding programs and selection for one does not adversely influence the other.

In the last 40 years, many experiments were carried out to produce new lines following the previous selection criteria. The start was in France followed by Spain, then in many countries all over the world. We mention the involvement of the INRA in France, and the Department of Animal Science of the Universidad Politécnica de Valencia (UPV) and the Rabbit Science Unit (IRTA, Barcelona) in Spain, developing lines to be used in crosses. In France, since the seventies, the INRA (SAGA, Toulouse) has been selecting two maternal lines for litter size traits (INRA1077 and INRA2066). Later, other new lines have been developed (INRA2666 and INRA1777). Concerning maternal lines in Spain, there are four maternal lines (A, V, H and LP) in UPV and one in IRTA (Prat) (Baselga, 2004; Khalil and Al-Saef, 2008). A brief list of these lines showing their types, origins and criteria of selection is presented in Table 1. A more complete list of maternal lines can be found in Garreau *et al.* (2004).

Line	Origin ¹	Criteria ²	Reference	Country
INRA1077	NZW, B	LSW	Rouvier, 1981	France
INRA2066	CAL, GH	LSB	Brun, 1993	France
INRA2666	INRA2066, V	LSW	Brun et al., 1998	France
А	NZW	LSW	Estany <i>et al.</i> , 1989	Spain
V	4 specialized maternal lines	LSW	Estany et al., 1989	Spain
Н	Commercial farms	(Hyperprolificacy), LSW	García-Ximénez et al., 1996	Spain
LP	Commercial farms	(Hyperlongevity), LSW	Sánchez, 2005	Spain
Prat	crossbreds	crossbreds LSW		Spain
APRI	BR, V	LWW	Youssef et al., 2008	Egypt
Uruguay-V	V	LSW	Capra <i>et al.</i> , 2000	Uruguay

Table 1: List of some specialized maternal lines selected in different countries

¹: The breed or the line of origin. NZW: New Zealand White; BR: Baladi Red; B: Bousct; GH: Gaint Himalayian; ²: The criteria of selection (foundation) of the line. LSW: litter size at weaning; LSB: litter size at birth; LWW: litter weight at weaning

We will give more details of the Spanish program specially the program of Universidad Politécnica de Valencia for development of new specialized lines. This program was started in 1976 and now there are four maternal and one paternal line, which are under selection.

Line A was founded in 1976 sampling NZW rabbits, reared by farmers near Valencia (Spain). After three generations without selection, the line has been selected by a family index (Baselga, 1984; Estany *et al.*, 1989) to increase litter size at weaning. Now generation 39 has been reached and the line is kept closed since its foundation.

Line V was founded in 1981 as a synthetic line of four specialised maternal lines. After three generations without selection, the line has been selected (Estany *et al.*, 1989) to increase litter size at weaning. The method of evaluating the animals is a BLUP under an animal-repeatability model. Now generation 35 has been reached and the line is kept closed since its foundation.

Line H was founded applying hyperprolific selection and embryo cryopreservation techniques (García-Ximénez et al., 1996). The hyperprolific does were assembled from a large commercial population, spread over different Spanish farms. The hyperprolific does were required to satisfy one or both of the following criteria: to have 17 or more young born alive in one litter or to have a cumulative number of young born alive in all recorded parities equal or higher to the threshold corresponding to the best 1% does of a population with a mean of 9 rabbits born alive per litter, a standard deviation of 2.65 rabbits/litter and a repeatability of 0.2. A first step was carried out in 1993 to obtain male progeny (VH males) by hysterectomy from 20 hyperprolific does mated to nine bucks of the different nuclei of line V, line showing a high prolificacy (Baselga et al., 1992). In a second step, a new and larger set of hyperprolific does (87 does) was mated to 47 VH males to obtain progeny (464 animals of 63 days) which constituted generation 0 of line H. Now, generation 17 has been reached and after its foundation the criteria of selection has been litter size at weaning.

The line LP was founded selecting does at commercial farms excelling because of their high longevity but being above the mean in prolificacy (Sánchez, 2005 and Sánchez *et al.*, 2008). It was intended to apply a very high intensity of selection for longevity, in a similar way as it was done in rabbits (Cifre *et al.*, 1998) or pigs (Bichard and David, 1985; Sorensen and Vernersen, 1991; Herm *et al.*, 1994; Noguera *et al.*, 1997) for prolificacy.

The foundation of the LP line took place in three steps and started in April 2002. The first step tried to get sons of LP does, 15 LP does detected in 8 commercial farms. The does were inseminated with semen from bucks of the current generation (27) of the V line.

The second step tried to get sons of a new batch of LP does mated to the males got in the first step. Another set of 15 LP does was selected and housed in the same lazaretto than the previous batch.

The third step was the constitution of the line LP with the progeny of 32 new LP does, detected in 25 farms of Spain and Portugal, mated to 17 bucks obtained in the previous step. Now, generation 5 has been reached and after the foundation LP line is being selected for litter size at weaning (Sánchez, 2005).

1.2.1.1.LITTER SIZE

Litter size is an important component of productivity in rabbit. Genetic improvement of litter size is an effective way of improving the economic efficiency in rabbit production (Baselga and Blasco, 1989; Armero and Blasco, 1992; Blasco et al., 1993; Blasco, 1996). Litter size at birth or litter size at weaning have been the objective of selection in several experiments involving rabbit populations (Baselga et al., 1992; de Rochambeau et al., 1994, 1998; Gómez et al., 1996). However, response to selection, when estimated, has been low (Rochambeau et al., 1994; García and Baselga, 2002a, b). In the same context, Armero et al. (1995) reported that litter size at birth or weaning have been the traits of choice to select specialized dam lines in meat rabbit production. Also, Santacreu (2002) reported that litter size is easy and not expensive to measure. The criteria of selection used are number of kits born alive or number of kits at weaning. These traits have a high genetic correlation with the number of kits at slaughter (García and Baselga, 2002b; Abou Khadiga, 2008). Litter size has a low heritability, but is highly variable, so that the additive genetic variability is far from negligible (Blasco et al., 1993) and significant genetic variation also exists between breeds and populations.

Genetic parameters

The estimation of variance components and genetic parameters of litter size traits is very important to establish their breeding program, to predict how much we can improve these traits and for monitoring the process of selection along the time.

The models used for the genetic analysis and evaluation of these traits in animals are, commonly, animal models of repeatability.

Heritability and repeatability

Reviewed estimates of heritability and repeatability for litter size traits are presented in Table 2, where it can be seen that the estimates used to be lower than 0.15 for the heritability and lower than 0.25 for the repeatability. The average of the estimates for total born (TB) and number born alive (NBA) are a little higher than for number weaned (NW) or number marketed (NM).

Permanent environmental effects

Generally, the ratio between the variance of permanent environmental effects and phenotypic variance (p^2) is between 10 and 20% (Gómez *et al.*, 1996; Lukefahr and Hamilton, 2000; Rochambeau, 1997; Rastogi *et al.*, 2000; García and Baselga, 2002a, b). Lower estimates of p^2 have been reported by Ferraz *et al.* (1992), Baselga *et al.* (2003) and Costa *et al.* (2004). Higher estimates have been obtained by Al-Saef *et al.* (2008).

animal models for fitter size traits in fabbits								
Traits	h^2	r	Breeds (lines)	References				
	0.07 0.03	0.19 0.17	A V	Baselga et al. (1992)				
	-	0.10	NZW, CAL	Ferraz et al. (1992)				
	0.20	0.25	NZW	Ayate <i>et al.</i> (1995)				
	0.08 0.08	-	CAL NZW	Ferraz and Eler (1996)				
	0.13	0.21	NZW, CAL	Lukefahr and Hamilton (1997)				
	0.08	015	Н	Cifre et al. (1998)				
	0.08	-	V	El-Raffa (2000)				
	0.06	-	PW	Garreau et al. (2000)				
	0.10	-	Caldes	Gómez et al. (2000)				
	0.09	0.30	NZW	Rastogi et al. (2000)				
	0.15	0.23	А	García (2000)				
ТВ	0.07	0.22	V	Garcia (2000)				
	0.19	0.19	Danish white	Sorensen et al. (2001)				
	0.10	0.22	V	García and Baselga (2002a)				
	0.15	0.24	Α	García and Baselga (2002b)				
	0.14	-	А					
	0.11		Prat	Piles et al. (2006)				
	0.10		V					
	0.04	0.22	V, SG	Al-Saef et al. (2008)				
	0.08	0.13	CPC-Italy	Mantovani et al. (2008)				
	0.01	0.34	APRI, V	Youssef <i>et al.</i> (2008)				
	0.09	0.21	V	Abou Khadiga (2008)				

Table 2: Reviewed estimates of heritability (h²) and repeatability (r) estimated by animal models for litter size traits in rabbits

Traits	h ²	r	Breeds (lines)	References
	0.06	-	NZW, CAL	Ferraz et al. (1992)
	0.07	0.19	А	Baselga et al. (1992)
	0.03	0.17	V	Dasciga <i>et ut</i> . (1992)
	0.08 0.11	-	NZW CAL	Afifi and Khalil (1992)
	0.27 0.12	-	NZW HL	Krogmeier et al. (1994)
	0.07 0.06	-	A1077 A2066	Rochambeau et al. (1994)
	0.09 0.03	-	CAL NZW	Ferraz and Eler (1996)
	0.08	0.15	Н	Cifre et al. (1998)
	0.07	-	Caldes	Gómez et al. (2000)
	0.12	0.32	NZW	Rastogi et al. (2000)
BA	0.05	-	Botucatu	Moura <i>et al.</i> (2001)
DA	0.13 0.07	-	A V	Baselga and García (2002)
	0.07	-	A1077	Bolet and Saleil (2002a)
	0.06	-	A2066	Bolet and Saleil (2002b)
	0.07	-	A9077	Bolet and Saleil (2002c)
	0.07	0.17	V	García and Baselga (2002a)
	0.13	0.21	А	García and Baselga (2002b)
	0.12	-	А	
	0.08	-	Prat	Piles et al. (2006)
	0.07	-	V	
	0.015	-	LP	Sánchez (2006)
	0.07 0.11	0.19 0.30	V APRI	Abou Khadiga (2008)
	0.05	0.11	CPC-Italy	Mantovani et al. (2008)

 Table 2: Cont.

Table	2:	Cont.
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Traits	h ²	r	Breeds (lines)	References
	0.07 0.02	0.13 0.10	A V	Baselga et al. (1992)
	0.11	-	NZW	Afifi and Khalil (1992)
	0.10	_	NZW-CAL	Ferraz and Eler (1994)
	0.23 0.05	-	NZW HL	Krogmeier <i>et al.</i> (1994)
	0.08	0.13	A1077	Rochambeau et al. (1994)
	0.08	0.13	NZW	Ayate <i>et al.</i> (1994)
	0.09	0.12		Ayate <i>et al.</i> (1993)
	0.00	-	NZW CAL	Ferraz and Eler (1996)
-	0.04	-	Prat	Gómez et al. (1996)
	0.06	-	NZW, CAL	Lukefahr and Hamilton (1997)
	0.06	0.12	Н	Cifre <i>et al.</i> (1998)
	0.04	-	A2066	Rochambeau et al. (1998)
	0.03	-	Caldes	Gómez et al. (2000)
NW	0.09	0.25	NZW	Rastogi et al. (2000)
-	0.03	-	Botucatu	Moura et al. (2001)
	0.08	-	Danish white	Sorensen et al. (2001)
	0.04	-	A1077	Bolet and Saleil (2002a)
	0.04	-	A2066	Bolet and Saleil (2002b)
	0.04	-	A9077	Bolet and Saleil (2002c)
	0.05	0.13	V	García and Baselga (2002a)
	0.11	0.17	А	García and Baselga (2002b)
	0.11		А	
	0.06 0.04	-	Prat V	Piles et al. (2006)
	0.08	_	LP	Sánchez (2006)
	0.05	0.16	V, SG	Al-Saef <i>et al.</i> (2008)
	0.01	0.20	APRI, V	Youssef et al. (2008b)
	0.06	0.15	V	
	0.09	0.27	APRI	Abou Khadiga (2008)
	0.07	0.12	А	Baselga at al. (1002
	0.01	0.08	V	Baselga et al. (1992
	0.06	0.11	Н	Cifre <i>et al.</i> (1998)
NM	0.05	0.12	V	García and Baselga (2002a)
	0.12	0.17	А	García and Baselga (2002b)
	0.03	0.09	V	Abou Khadiga (2008)
	0.05	0.12	APRI	Abbu Kilaulga (2008)

TB: Total born; BA: Number born alive; NW: Number weaned; NM: Number marketed; CAL: California; NZW: New Zealand White: SG: Saudi Gabali; WP: White Pannon; HL: Helle Grosilber.

Selection response for litter size

It has not been easy to detect responses in programmes of selection for litter size, excepting in mice, where Nielsen (1994) reported a significant response. A significant response in pigs has been demonstrated in few cases, such as the experiment reported by Lamberson *et al.* (1991) or the ones related to selection on hyperprolificacy (Bichard and David, 1985; Sorensen and Vernensen, 1991; Bidanel *et al.*, 1994; or Noguera *et al.*, 1997). In general, the genetic progress of litter size at birth in pigs has been lower

than expected (Southwood and Kennedy, 1991; Wang *et al.*, 1994). Besides, Lamberson and Day (1986) and Casey *et al.* (1994) did not observe a correlated response in litter size when selection was for ovulation rate, despite the significant direct response.

In rabbit, use of maternal lines based on selection for hyperprolificacy has been a successful way to improve litter size (Cifre *et al.*, 1998).

Significant genetic trends in litter size have been reported when mixed model methodology (Sorensen and Kennedy, 1986) has been used to analyse the long and medium term experiments of selection for litter size, but the result of this methodology is model and genetic parameter dependent.

Some responses in litter size traits were estimated exclusively by mixed-model methods (Estany *et al.*, 1989; Rochambeau *et al.*, 1994; Gómez *et al.*, 1996) and the estimates ranged from 0.05 to 0.13 rabbits born alive or weaned per litter and generation. With the same method García and Baselga (2002a, b) found that the genetic trend was 0.175 weaned per generation in line A and 0.09 in line V. Analysis of the responses to selection by comparison to a control population (Rochambeau *et al.*, 1998; Tudela *et al.*, 2003) or by the use of frozen embryos (García and Baselga, 2002a, 2002b), estimated responses between 0.08 and 0.09 rabbits total born, born alive or weaned per litter and generation.

Baselga (2004) noted that causes of obtained responses lower than expected could be:

- (1) Low estimates of additive genetic variance for litter size at weaning.
- (2) Heterogeneity among parities that can be high.
- (3) Negative correlations between direct and maternal effects.
- (4) Low selection intensity.

Concerning correlated response, selection for ovulation rate was associated with a correlated increase in litter size, similar to the response obtained by direct selection (Ibáñez-Escriche *et al.*, 2004; Laborda *et al.*, 2008). Ibáñez-Escriche *et al.* (2004, 2006) and Laborda *et al.* (2008) reported values of direct response for ovulation rate of 0.97, 1.8 and 1.5 ova and correlated responses values for total born of 0.32, 0.49 and 0.4. These estimates were obtained, without control line, using a Bayesian approach. After 10 generations of divergent selection for uterine capacity, the correlated response obtained by Santacreu *et al.*, (2005) for total born between high and low lines was 2.35 rabbits, mainly because of a higher correlated response in the low line (1.88 rabbits).

But, they reported that, although selection for uterine capacity has been proposed as an indirect way of improving litter size (Bennett and Leymaster, 1989; Argente *et al.*, 1997, 2000; Blasco et al., 2000, 2005), the observed increase in total born caused by selection for uterine capacity was not greater than the improvement obtained from direct selection and the correlated response in number born alive was less than for total born.

1.2.1.2.KINDLING INTERVAL

We defined this trait as the number of days between two consecutives parities. Kindling interval is economically important and is a direct indicator of the fertility of the does for a given mating management.

Significant differences in direct genetic effects between lines were found for kindling interval (Baselga *et al.*, 2003). Also, they found that the heritability and ratio of variance of environmental permanent effects to phenotypic variance of this trait were 0.078 and 0.008, respectively. Khalil and Soliman (1989) and Moura *et al.* (2001) estimated the heritability of the interval between parities and obtained values that were close to zero.

1.3. INBREEDING DEPRESSION

Wright's (1922) coefficient of inbreeding (F) describes the probability that 2 alleles at any locus are identical by descent. Inbred offspring result from mating two animals which have one or more common ancestors. Breeders of livestock perceive inbreeding as being deleterious and consequently try to avoid the mating between close relatives. This leads to an increase in homozygosity and to the corresponding decrease in heterozygosity of the population.

With almost no exception, empirical studies indicate that inbreeding causes an unfavourable shift of the mean phenotypic value shown by characters connected with reproductive capacity or physiological efficiency. This phenomenon is known as inbreeding depression (Wright, 1977; Shields, 1982; Charlesworth and Charlesworth, 1987; Ralls *et al.*, 1988; Lynch, 1989). The amount of inbreeding is accumulated in a finite population and reduces genetic variance available for selection in later generations (Falconer and Mackay, 1996).

In rabbit, Moura *et al.* (2000) have estimated the reduction in litter size at birth and at weaning caused by a 10% of inbreeding of the doe: 0.81 and 0.59 young per litter respectively. In the same context, Chai (1961), Ferraz (1991) and Park *et al.* (1991) also

noted a consistent reduction in litter size at birth and at weaning as a consequence of inbreeding. The inbreeding depression of litter size in mice was demonstrated long time ago (Falconer, 1960).

2. OBJECTIVES

The principal objective of this study is the comparison between four Spanish maternal lines of rabbit (A, V, H and LP lines) for litter size traits (total born, number born alive, litter size at weaning and litter size at marketing) and kindling interval, taking into account all the information recorded since their foundation.

To achieve this objective we go through the following steps:

- a. Estimate the inbreeding coefficient of the animals, to include it into the models, trying to estimate the inbreeding depression.
- b. Estimate the genetic parameters of litter size traits and kindling interval, needed to solve the animal mixed models proposed for these traits.
- c. Estimate the difference between the founder generations of the A, V, H and LP lines for litter size traits and kindling interval. These comparisons rely on the solution of the animal mixed models.
- d. Compare, at fixed times, the lines for litter size traits and kindling interval. The times chosen for the comparisons are the last six seasons shared at the same farm by at least three lines. From December 2002 to May 2004 for the lines A, V and H and from September 2007 to February 2009 for the lines A, V and LP. These comparisons are tried to be non dependent of the genetic models of the traits and use, only, the records obtained during the times of comparison.

3. MATERIALS AND METHODS

3.1. ANIMALS

The present study was conducted on four Spanish maternal lines of rabbit, A, V, H and LP. The following sections describe the management and the selection process.

3.1.1. FLOCK MANAGEMENT

The animals of A, V and LP lines have been housed since the beginning of the selection process until now at the farm of the Animal Science Department, Universidad Politécnica de Valencia, as a closed nucleus of selection. The H line was housed at the same farm until the 10th generation of selection and at this moment (May 2004) it was moved to a different farm 180 km north of Valencia (San Carlos de la Rápita, Tarragona).

The first mating of the does was around 17 weeks of age. The does were serviced 10-12 days post kindling by its assigned buck. So, the minimum interval between parities was 42 days. Each doe was transferred to the assigned buck to be mated and returned back again to her own cage. On the day 12 post mating, each doe was palpated to detect pregnancy. Doe that was not pregnant was returned to new mating. It was tried to avoid the mating between close relatives and the mates should not have common grandparents. The maximum number of weekly services allowed to a buck was three.

Three days before the expected day for kindling, the nest boxes were prepared. Litters born were examined and recorded for total born and number born alive. The litters born stayed with their mothers, without fostering, for about 28 days. At this moment the weaning took place and the rabbits were individually identified by a number tattooed on the ear. Rabbits fed standard pelleted diet, offered *ad libitum*.

3.1.2. The line A

The A line is a maternal line. It is selected since 1980 to increase the litter size at weaning by a family index (Baselga, 1984; Estany *et al.*, 1989). Its analysis included the data from the 1^{st} generation to the 38^{th} generation. The number of bucks per generation was around 25. The number of breeding does and the number of does actually contributing with progeny to the next generation are shown in Table 3. The crude means of litter size at weaning for these set of bucks and does are also shown.

Table 3: Number of bucks, does, litters and crude means of litter size (Mean) at wea	aning
by generation. Line A	

Commission	All does			Bucks and Does contributing to the next generation			
Generation	NT 1	T	7	D 1			
	Number	Litters	Mean	Bucks	Does	Litters	Mean
1	92	235	5.25	16	25	74	6.88
2	116	302	5.74	14	33	109	6.82
3	106	339	4.43	17	40	161	5.06
4	97	207	4.66	20	49	122	5.45
5	67	128	6.23	16	44	93	6.68
6	115	230	6.08	21	48	116	7.17
7	146	382	5.76	20	46	168	6.51
8	123	344	5.72	16	38	152	6.55
9	110	252	5.91	14	35	112	6.71
10	128	341	6.12	18	31	107	7.31
11	156	422	6.12	20	45	173	7.01
12	141	404	6.15	24	36	154	6.9
13	121	317	6.59	17	41	134	7.63
14	126	387	6.48	23	48	177	7.02
15	132	470	7.11	25	58	239	7.95
16	159	494	7.1	27	55	184	7.88
17	121	425	6.97	27	43	154	8
18	115	436	7.11	25	52	234	7.82
19	128	528	6.67	23	52	282	7.3
20	200	697	7.2	22	55	268	7.83
21	132	435	7.26	25	48	198	7.98
22	114	370	7.25	25	50	199	7.97
23	118	355	8.18	24	50	176	8.93
24	117	342	7.7	25	39	146	8.82
25	104	340	7.47	26	46	174	8.34
26	237	661	7.7	36	134	383	8.29
27	123	392	7.53	25	42	167	8.44
28	122	426	8.16	26	41	160	8.63
29	105	375	7.81	25	49	191	8.61
30	136	540	7.73	25	47	227	8.58
31	125	629	7.19	23	47	278	7.81
32	149	552	7.78	23	48	224	8.19
33	122	492	7.73	20	43	196	8.51
34	137	552	8.28	25	53	238	9.01
35	143	656	8.07	21	51	280	8.96
36	135	539	7.91	25	43	195	9
37	119	497	8.53	21	34	167	9.38
38	116	342	8.63	-	-	-	-

The selection was in non overlapping generations and the does for the next generation were selected from the best evaluated matings. The bucks were selected within sire from the best mating, trying that each sire contributed with a son to the next generation.

3.1.3. The line V

The V is a maternal line. It was founded in 1984 at Universidad Politécnica de Valencia. The line has been selected to increase litter size at weaning (Estany *et al.*, 1989). The method of evaluating the animals was BLUP under a repeatability animal model. Its analysis included the data from the 1st generation to the 34th generation. The number of bucks per generation was around 25. The number of breeding does and the number of does actually contributing with progeny to the next generation are shown in Table 4. The crude means of litter size at weaning for these set of bucks and does are also shown.

Table 4: Number of bucks, does, litters and crude means of litter size (Mean) at weaning by generation. Line V

Generation				Bucks as	nd does con gener	U	the next
	Number	Litters	Mean	Bucks	Does	Litters	Mean
0	67	140	6.84	17	57	118	7.22
1	90	177	6.12	22	65	139	6.47
2	96	223	6.75	21	71	187	7.04
3	153	431	7.5	18	43	142	8.9
4	165	567	7.39	19	42	231	8.37
5	162	662	7.43	15	41	195	8.25
6	129	482	8.02	17	36	150	8.89
7	90	488	7.82	17	37	239	8.54
8	139	456	7.88	23	68	299	8.28
9	306	981	7.52	31	109	445	7.96
10	275	985	7.84	30	77	384	8.51
11	148	632	8.07	30	44	239	8.86
12	85	332	7.71	25	38	172	7.87
13	112	468	7.36	23	41	211	8.22
14	103	488	7.84	23	44	227	8.54
15	105	456	7.78	21	42	210	8.75
16	146	593	7.8	28	62	312	8.47
17	213	644	8.14	30	68	227	9.16
18	149	528	8.34	25	61	249	8.96
19	113	382	8.03	25	50	183	9.16
20	138	569	8.4	26	52	230	8.92
21	304	1091	8.28	34	96	305	8.66
22	155	514	8.39	22	48	189	9.2
23	125	420	8.1	26	58	213	8.88
24	189	616	8.43	20	56	207	9.24
25	131	538	8.98	22	40	202	9.23
26	138	528	8.69	23	50	215	9.51
27	108	294	8.56	19	40	107	8.96
28	137	560	9	24	49	236	9.8
29	132	528	8.29	25	51	348	8.84
30	174	957	8.06	28	98	676	8.76
31	165	1183	7.48	25	62	567	8.1
32	144	717	7.87	20	43	256	8.51
33	131	542	8.74	18	42	235	9.79
34	147	604	8.2	-	-	-	-

The selection was in non overlapping generations and the does for the next generation were selected from the best evaluated matings. The bucks were selected within sire from the best mating, trying that each sire contributed with a son to the next generation.

3.1.4. The line **H**

The H line is a maternal line founded in 1995 by hyperprolific selection principles (García-Ximénez *et al.*, 1996) and after its foundation the criteria of selection has been litter size at weaning. The method of evaluating the animals was BLUP under a repeatability animal model. Its analysis included the data from the 1st generation to the 15th generation. The number of bucks per generation was around 25. The number of breeding does and the number of does actually contributing with progeny to the next generation are shown in Table 5. The crude means of litter size at weaning for these set of bucks and does are also shown.

Generation	All does			Bucks and Does contributing to the next generation			
	Number	Litters	Mean	Buck	Does	Litters	Mean
1	136	459	8.81	25	40	172	9.65
2	87	202	7.58	26	81	191	7.75
3	126	372	8.57	21	38	126	9.48
4	93	297	8.66	15	34	131	9.79
5	132	459	8.1	20	48	162	9.94
6	141	478	7.9	22	51	197	8.48
7	135	472	8.05	19	41	139	8.68
8	137	559	8.7	21	39	174	9.81
9	138	505	8.34	19	44	187	9.09
10	124	541	7.55	24	42	250	8.23
11	113	554	7.83	25	45	249	8.69
12	149	850	8.41	22	51	369	9.04
13	178	894	8.09	23	56	352	9.26
14	178	1012	8.49	23	63	416	9.71
15	208	923	8.82	-	-	-	-

Table 5: Number of bucks, does, litters and crude means of litter size (Mean) at weaning by generation. Line H

The selection was in non overlapping generations and the does for the next generation was selected from the best evaluated matings. The bucks were selected within sire from the best mating, trying that each sire contributed with a son to the next generation.

3.1.5. The line LP

The LP line is a maternal line and it was founded by selecting females from commercial farms that showed extremely high productive lives (measured as a number of parities), but 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, 2005 and Sánchez *et al.*, 2008). Its analysis included the data from the 1st generation to the 4th generation. The number of bucks per generation was around 25. The number of breeding does and the number of does actually contributing with progeny to the next generation are shown in Table 6. The crude means of litter size at weaning for these set of bucks and does are also shown.

Table 6: Number of bucks, does, litters and crude means of litter size (Mean) at weaning by generation. Line LP

Generation		All does		Bucks and Does contributing to the next generation						
	Number	Litters	Mean	Bucks	Number	Litters	Mean			
1	299	1874	7.95	26	47	462	8.69			
2	142	701	8.74	66	41	265	9.53			
3	139	658	8.53	47	31	169	9.41			
4	104	171	8.27	-	-	-	-			

The selection was in non overlapping generations and the does for the next generation were selected from the best evaluated matings. The bucks were selected within sire from the best mating, trying that each sire contributed with a son to the next generation.

3.2. INBREEDING COEFFICIENT

The inbreeding coefficient was calculated by using the recursive algorithm described by Tier (1990).

3.3. STUDIED TRAITS

The analysis was performed for the inbreeding coefficient (\mathbf{F}) , litter size traits and kindling interval.

Litter size traits

-TB: Total born.

-BA: Number born alive.

-NW: Number weaned.

-NM: Number marketed (at 63 days of age).

Kindling interval

-KI: Number of days between two consecutives parities.

3.4. STATISTICAL ANALYSIS

3.4.1. GENETIC ANALYSIS

Data from all generations for all lines were used in the analysis. A total of 47132 parities were analysed (15878, 19280, 8570 and 3404 parities for A, V, H and LP, respectively). The pedigree file included 14609 individuals.

- Litter size

The variance components of the random effects were estimated by REML, using the data of the four maternal lines all together and the version 6.0 of the VCE software (Groeneveld *et al.*, 2008). Two-trait repeatability animal models were considered. As selection was applied for litter size at weaning, this trait was included in every analysis in order to obtain parameter estimates, excepting itself (NW) that was analyzed alone.

The model used for the trait t of litter size was as follows:

 $y_{tijklmn} = AE_{ti} + EF_{tj} + L_{tk} + AEL_{tl} + F_{tm} + a_{tn} + p_{tn} + e_{tijklmn}$ where;

y_{tijklmn} is a record of the trait t of litter size

 AE_{ti} is a fixed effect, farm-year-season of the parity (one year season every three months: 132 levels for all traits and 115 levels for NM),

 EF_{tj} is a fixed effect, physiological state of the doe (5 levels depending on the parity order and lactation state at the moment of positive insemination): 1 for nulliparous, 2 (4) for primiparous lactating (no lactating), 3 (5) for multiparous lactating (no lactating) does,

 L_{tk} is a fixed effect, line effect (4 levels)

 AEL_{tl} is a fixed effect, interaction between farm-year-season and line (291 levels for TB, BA and NW, and 265 levels for NM),

 F_{tm} is a fixed effect, the inbreeding effect (7 levels depending on the inbreeding level): 1 from 0 to 0.05, 2 from 0.05 to 0.10, 3 from 0.10 to 0.15, 4 from 0.15 to 0.20, 5 from 0.20 to 0.25, 6 from 0.25 to 0.30, 7 from 0.30 to 0.35,

 a_{tn} is a random effect, the additive value of the doe n,

 p_{tn} is a random effect, the permanent environmental effect of the doe n,

e_{tijklmn} is a random effect, residual of the model.

Inbreeding was used as a fixed effect after dividing it into categories, as previously explained, in order to minimize the problem of its co-linearity with farm-year-seasons.

The model represented in matrix form for the trait t is as follows:

 $\mathbf{y}_t = \mathbf{X}_t \mathbf{b}_t + \mathbf{Z}_{1t} \mathbf{a}_t + \mathbf{Z}_{2t} \mathbf{p}_t + \mathbf{e}_t,$

 y_t is the vector of observations, $E(y_t) = Xb$,

 \mathbf{X}_t is the incidence matrix of the fixed effects,

 $\mathbf{b}_{\mathbf{t}}$ is the vector of fixed effects,

 \mathbf{Z}_{1t} is the incidence matrix of the additive values,

 \mathbf{a}_t is the vector of additive values, $\mathbf{E}(\mathbf{a}_t)=\mathbf{0}$,

 \mathbf{Z}_{2t} is the incidence matrix of the permanent environmental effects,

 \mathbf{p}_t is the vector of permanent environmental effects, $\mathbf{E}(\mathbf{p}_t)=\mathbf{0}$,

 e_t is the vector of residuals, $E(e_t)=0$.

The variance and covariance of random effects are:

$$V(\mathbf{a}_{t}) = \mathbf{A} \sigma_{at}^{2}$$

$$V(\mathbf{p}_{t}) = \mathbf{I} \sigma_{pt}^{2}$$

$$V(\mathbf{e}_{t}) = \mathbf{I} \sigma_{et}^{2}$$

$$Cov (\mathbf{a}_{i}, \mathbf{a}_{j}) = \mathbf{A} r_{gij} \sigma_{ai} \sigma_{aj}$$

$$Cov (\mathbf{p}_{i}, \mathbf{p}_{j}) = \mathbf{I} r_{pij} \sigma_{pi} \sigma_{pj}$$

$$Cov (\mathbf{e}_{i}, \mathbf{e}_{j}) = \mathbf{I} r_{eij} \sigma_{ei} \sigma_{ej}$$
where:

 σ^2_{at} is the additive variance for the trait t,

 σ^2_{pt} is the permanent environmental variance for the trait t

 σ^2_{et} is the residual variance for the trait t

r_{gij} is the genetic correlation between the traits i and j,

 r_{pij} is the permanent environmental correlation between the traits i and j,

 r_{eij} is the residual correlation between the traits i and j,

A, is the numerator relationship matrix; I, is a identity matrix.

- Kindling interval

Variance and covariance components for kindling interval were estimated by a two-trait repeatability animal model being the other trait the litter size at weaning.

The model used for kindling interval was as follows:

 $y_{ijklmn} = AE_i + OP_j + L_k + AEL_l + F_m + a_n + p_n + e_{ijklmn}$ where;

y_{ijklmn} is a record of kindling interval,

 AE_i is a fixed effect, farm-year-season of the parity (one year season every three months: 131 levels),

OP₁ is a fixed effect, parity order of the doe (14 levels),

 L_k is a fixed effect, line effect (4 levels)

 AEL_1 is a fixed effect, interaction between farm-year-season and line (289 levels),

F_m is a fixed effect, the inbreeding effect (7 levels),

 a_n is a random effect, the additive value of the doe n,

 p_n is a random effect, the permanent environmental effects of the doe,

e_{ijklmn} is a random effect, residual of the model.

The structure of the co-variance between the random effects of the kindling interval and litter size at weaning was similar to the structure showed before for two traits of litter size.

3.4.2. COMPARISON AT THE ORIGIN OF LINES

The same models and data showed in the previous section were used to estimate the performance level of the A, V, H and LP lines at their origin. The mixed model equations were solved using the variances and covariances estimated, as explained in the previous section, using the PEST software package (Groeneveld, 1990).

The contrasts between two lines were estimable functions involving the estimates of the line effects and the estimates of the interactions farm-year-season-line, corresponding to all the farm-year-seasons shared by the two lines. For each line and trait was computed a variable: the sum of the line effect and the average of the interactions farm-year-season-line corresponding to the line and farm-year-seasons shared. The contrast was the difference between the variables computed for each line.

The farm-year-seasons shared between the lines were: 9 to 115 (June 1982 to February 2009, at the UPV farm) for the A and V lines, 65 to 96 (June 1996 to June

2004 at the UPV farm) for the lines A or V and H, and 95 to 115 (December 2003 to February 2009, at the UPV farm) for the A or V and LP lines.

Significance was claimed at a first class error, α =0.05.

3.4.3. COMPARISON AT FIXED TIMES

The times chosen for the comparisons were the last six seasons shared at the same farm by at least three lines: from December 2002 to May 2004 for the lines A, V and H and from September 2007 to February 2009 for the lines A, V and LP. These comparisons are tried to be non dependent of the genetic models of the traits (the additive effects were excluded from the models) and used, only, the records obtained during the times of comparison. All the models were solved using the PEST software package (Groeneveld, 1990) to analyze the data and estimate the contrast between lines.

Thus, the statistical models used in this analysis were the same models used in the previous section, but the additive effects were not considered. Concerning the variance components used for solving the models, the permanent variance in this analysis was the sum of the additive variance and the permanent variance of the previous analysis. The residual variance used was the same in both analyses.

The estimable functions used for the contrasts were computed as explained in the previous section and the first class error was set at α =0.05.

4. **RESULTS AND DISCUSSION**

4.1. **Descriptive statistics**

The mean and the standard deviation for litter size traits and kindling interval are shown in Table 7. All parities of the 12639 does, of the four lines, along the selection process, were considered to compute the general descriptive statistics.

The high prolificacy demonstrated by all lines should be noted. These lines had a high mean of litter size at weaning and these means were improved along the time as can be guessed in Tables 3, 4, 5 and 6. Thus, the litter size mean at weaning of the A line increased 3.38 young from the 1st to the 38th generation. Also, the V line started with a mean of 6.84 rabbits weaned and it was 8.20 young at 34th generation. Line LP started with 7.95 and now was 8.27 young (4th generation).These changes could be due to a response to the selection for litter size (García and Baselga 2002 a, b) and to changes in feeding, management, equipment or others.

The present results of litter size at different ages were in the range of reviewed estimates (García and Baselga 2002a, b; Costa *et al.*, 2004; Theilgaard *et al.*, 2007; Al-Saef *et al.*, 2008; Sánchez *et al.*, 2008).

Bolet and Saleil (2002a, b, c) reported, for the INRA1077, INRA2066 and INRA9077 lines, the following means for total born (number weaned): 8.5 (6.4), 9.1 (7.6) and 7.3 (5.5), respectively.

Table 7: Basic statistics for litter size traits (rabbits) and kindling interval (days) (Mean,standard deviation (SD) and extreme values)

Trait	N	Mean	SD	Minimum	Maximum
Total born	47132	9.80	3.07	1.00	26.00
Number born alive	47132	9.07	3.36	0.00	22.00
Number weaned	47097	7.79	3.05	0.00	18.00
Number marketed	43265	6.95	3.25	0.00	16.00
Kindling interval	34356	49.80	11.48	37.00	99.00

N: number of records

4.2. INBREEDING COEFFICIENT

The minimum, maximum and mean of the inbreeding coefficient for A, V and H lines by generation are shown in Tables 8, 9 and 10. The inbreeding coefficient for the animals of the LP line was equal zero because the line was still in the 4th generation of selection.

The inbreeding mean increased along the selection, so that the mean of the inbreeding coefficient reached 0.30 at generation 38 of the line A, 0.25 at generation 34 of the line V and 0.14 at generation 16 of the line H.

These figures allow the computation of an effective population size (N_e) for each line, applying the formula,

 $F_t = 1 - [1 - 1/(2N_e)]^t$,

being F_t the inbreeding reached at the last generation, the generation t. N_e would be the size of a population with $N_e/2$ males and $N_e/2$ females that reproduces at random with the same probability of the animals of the parent generation to contribute to the next generation.

The resulting values of N_e were: 54 animals for line A, 59 animal for Line V and 47 animals for line H. We can compare these values with the expected N_e for these lines if the reproduction would have been at random without selection. The size of these lines was intended around 25 males and 125 females. The corresponding N_e would be given by the formula,

 $1/N_e = 1/4N_m + 1/4N_f$

where N_m is the number of males and N_f is the number of females. The result is 83, what corresponds to an increase per generation of 0.006 of the inbreeding coefficient. The actual increases have been 0.008 in the line A, 0.007 in the line V and 0.009 in the line H, all of them higher than 0.006, due to the effect of selection. Wray (1989) has developed formulas that predict the inbreeding in populations submitted to selection under a hierarchical structure of reproduction. She noted that the increase in inbreeding under selection could be several times the increase expected under random mating. In our case the effect of selection seems to be lower probably because the management followed to reduce the increase of the inbreeding. In material and methods it was explained that each male contributed with a son to the next generation and the matings were not at random but between mates do not sharing any grandparent. In fact, the number of males (N_{mi}) and females (N_{fi}) contributing progeny to generation i are known and we can compute the effective population size, N_{ei} , of this generation, assuming random mating and equal probability of giving progeny to the next generation. The value of N_{ei} would be,

 $1/N_{\rm ei} = 1/4N_{\rm mi} + 1/4N_{\rm fi}$,

that could be different from one generation to another. Accepting the same assumptions, it could be computed a constant value N_{ec} , that would produce the same inbreeding along the t generations. This value will be computed by the formula,

 $1/N_{ec} = 1/t (1/N_{e1} + 1/N_{e2} + 1/N_{e3} + ... + 1/_{Net-1} + 1/N_{et})$

The values found for the different lines were: 59 animals for line A, 60 animals for line V and 50 animals for line H. It is not expected that these values corresponds to the actual values of equivalent population sizes computed with the actual values of inbreeding at the last generation of selection (N_e), because the assumptions are not met. Table 8: Basic statistics of inbreeding coefficient for line A in all generations

Generation	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Minimum	0	0	0	0	0	0.01	0.02	0.03	0.04	0.06	0.07	0.08	0.10	0.11
Maximum	0	0	0	0.06	0.09	0.08	0.07	0.08	0.17	0.15	0.13	0.13	0.16	0.17
Mean	0	0	0	0.02	0.02	0.03	0.04	0.04	0.06	0.07	0.09	0.10	0.12	0.13
Generation	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Minimum	0.11	0.13	0.14	0.14	0.16	0.16	0.17	0.18	0.18	0.19	0.19	0.20	0.21	0.22
Maximum	0.16	0.17	0.19	0.18	0.21	0.20	0.22	0.23	0.23	0.22	0.25	0.27	0.24	0.34
Mean	0.13	0.14	0.15	0.16	0.17	0.18	0.18	0.19	0.20	0.21	0.21	0.22	0.22	0.23
Generation	29	30	31	32	33	34	35	36	37	38				
Minimum	0.22	0.23	0.23	0.24	0.25	0.26	0.26	0.27	0.28	0.29				
Maximum	0.25	0.27	0.27	0.34	0.28	0.29	0.29	0.30	0.31	0.31				
Mean	0.23	0.24	0.25	0.26	0.26	0.27	0.27	0.28	0.29	0.30				

Table 9: Basic statistics of inbreeding coefficient for line V in all generations

Generation	0	1	2	3	4	5	6	7	8	9	10	11	12	13
Minimum	0	0	0	0	0	0	0.02	0.02	0.03	0.05	0.06	0.07	0.08	0.09
Maximum	0	0	0.06	0.03	0.04	0.03	0.08	0.05	0.17	0.10	0.09	0.11	0.13	0.12
Mean	0	0	0	0	0.01	0.01	0.03	0.04	0.05	0.07	0.07	0.08	0.09	0.10
Generation	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Minimum	0.10	0.10	0.11	0.12	0.13	0.14	0.15	0.11	0.16	0.16	0.17	0.18	0.18	0.19
Maximum	0.16	0.13	0.17	0.18	0.20	0.25	0.18	0.21	0.21	0.23	0.20	0.24	0.23	0.24
Mean	0.11	0.11	0.13	0.13	0.14	0.16	0.16	0.17	0.17	0.19	0.18	0.19	0.20	0.21
Generation	28	29	30	31	32	33	34							
Minimum	0.20	0.21	0.21	0.22	0.22	0.23	0.24							
Maximum	0.23	0.26	0.27	0.25	0.25	0.26	0.27							
Mean	0.21	0.23	0.23	0.23	0.24	0.24	0.25							

Comparing, within line, both set of values (54 versus 59 for line A; 59 versus 60 for line V and 47 versus 50 for line H) the actual values are a little lower than the others. There are several reasons that could explain the differences between both values, N_e and N_{ec} . The effect of selection would be to do N_e lower than N_{ec} , but the opposite effect should be expected from the facts that the mating between relatives were avoided and

from the fact that all the males contribute with a son to the next generation and that the variance of the contribution of the females is lower that the variance under equal probability. In our case the effect of the selection dominated over the other effects but it was not far of being compensated.

Table 10: Basic statistics of inbreeding coefficient for line H in all generations.

Generation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Minimum	0	0	0	0	0	0	0.01	0.04	0.05	0.06	0.07	0.07	0.09	0.10	0.11	0.12
Maximum	0	0	0	0	0.03	0.13	0.13	0.08	0.18	0.12	0.15	0.12	0.15	0.14	0.17	0.15
Mean	0	0	0	0	0.01	0.02	0.04	0.05	0.07	0.08	0.09	0.09	0.11	0.12	0.13	0.14

4.3. GENETIC PARAMETERS

4.3.1. LITTER SIZE TRAITS

Heritability

Estimated genetic parameters of litter size for A, V, H and LP lines are presented in Table 11. All information of the four lines in the selection process was used to estimate the genetic parameters. The heritability estimates were rather low and tend to decrease from birth to slaughter. The heritability for total born was 0.14, for number born alive 0.10, for number weaned 0.08 and for number marketed was 0.08.

Table 11: Genetic parameters of litter size traits and kindling interval

Trait	h ²	p ²	r _g	r _p	r _e
Total born	0.14±0.01	0.10 ± 0.01	0.80±0.03	0.71±0.03	0.60 ± 0.00
Number born alive	0.10±0.01	0.10±0.02	0.90 ± 0.01	0.83 ± 0.02	0.81±0.00
Number weaned	0.08±0.01	0.08 ± 0.01	-	-	-
Number marketed	0.08±0.01	0.07 ± 0.01	0.96 ± 0.01	0.94 ± 0.01	0.91±0.00
Kindling interval	0.05±0.01	0.05±0.01	-0.24 ± 0.09	0.54 ± 0.07	-0.03±0.01

 h^2 : heritability, p^2 : ratio of the permanent environmental variance to the phenotypic variance, r_g : genetic correlation between number weaned and the trait, r_p : permanenet correlation between number weaned and the trait and r_e : residual correlation between the number weaned and the trait.

The heritability estimates of litter size traits reported in previous studies vary considerably. As a whole, the estimates are low to moderate. Some authors have found estimates similar to ours (Ayyat *et al.*, 1995; Lukefahr and Hamilton, 1997; Sorensen *et al.*, 2001; García and Baselga, 2002a, b; Piles *et al.*, 2006 and Abou Khadiga, 2008 for total born; Afifi and Khalil, 1992; Ferraz and Eler, 1996; Rochambeau *et al.*, 1994; Lukefahr *et al.*, 1996a; Gómez *et al.*, 1996; Piles et al., 2006 and Abou Khadiga, 2008,

for number born alive; Rochambeau *et al.*,1994; Ayyat *et al.*,1995; Rastogi *et al.*,2000; Sorensen *et al.*, 2001; Piles *et al.*, 2006; Sánchez, 2006; Abou Khadiga, 2008 for number weaned; Baselga *et al.*,1992 and Cifre *et al.*,1998 for number marketed).

Other authors have got estimates lower than ours for total born (Baselga *et al.*, 1992; Ferraz and Eler, 1996; Garreau *et al.*, 2000; García and Baselga, 2002a; Youssef *et al.*, 2008), number born alive (Baselga *et al.*, 1992; Ferraz *et al.*, 1992; Ferraz and Eler, 1996; Moura *et al.*, 2001; Mantovani *et al.*, 2008; Youssef *et al.*, 2008), number weaned (Baselga *et al.*, 1992; Ferraz and Eler, 1996; Gómez *et al.*, 1996; Moura *et al.*, 2001; Youssef *et al.*, 1992; García and Baselga, 2002b; Abou Khadiga, 2008).

Higher heritability estimates have been reported for number born alive, number weaned and number marketed by García and Baselga (2002b) and for number born alive by Sánchez *at al.* (2006).

Low heritabilities will be reflected in low responses to direct selection (≈ 0.10 rabbits per litter per generation; Baselga *et al.*, 1992; Poujardieu *et al.*, 1994; Rochambeau *et al.*, 1994; Gómez *et al.*, 1996; García and Baselga, 2002a). However, other studies (Mgheni and Christensen, 1985; Khalil *et al.*, 1987, 1988; Krogmeier *et al.*, 1994) reported moderate to high heritability values, but these estimates were associated with rather high standard errors.

It is well known that differences in heritability estimates could be attributed to the estimation method, strains, environmental effects or sampling error due to a small data set.

Permanent environmental effects

Estimates of permanent environmental effects for litter size traits in A, V, H and LP lines are presented in Table 11. They were low to moderate, very similar to the estimates of the heritability and seemed to decrease between birth and market time.

The repeatability (the sum of h^2 and p^2) was 0.24 for total born, 0.20 for number born alive, 0.16 for number weaned and 0.15 for number marketed.

Lukefahr and Hamilton (1997) and Sorensen *et al.* (2001) observed that permanent environmental effects were small and not significantly different from zero for litter size traits except for litter size at weaning. Similarly, Ayyat *et al.* (1995) showed that the differences between heritability and repeatability estimates were very small, reflecting very small permanent environmental effects. Similar results to our results were obtained by other authors for total born (Ayyat *et al.*, 1995; Lukefahr and Hamilton, 1997; García, 2000; García and Baselga, 2002a, b; Al-Saef *et al.*, 2008; Abou Khadiga, 2008), number born alive (Baselga *al.*, 1992; García and Baselga, 2002b; Abou Khadiga, 2008), number weaned (García and Baselga, 2002b; Sánchez *et al.*, 2006; Al-Saef *et al.*, 2008; Abou Khadiga, 2008) and number marketed (Baselga *et al.*, 1992; García and Baselga, 2002a, b).

Correlations

Genetic, permanent and residual correlations among litter size at weaning and the other litter size traits are presented in Table 11. The genetic correlation between number weaned and other litter size traits are positive and high (0.80 to 0.96), showing the closeness of the genetic determinism of these traits.

The permanent environmental correlations between litter size at weaning and total born, number born alive and number at marketing took high positive values (0.71, 0.83, and 0.94, respectively). The same pattern was also followed by the residual correlations and it shows, as it has been commented before for the genetic correlations, that these traits are very close.

The present estimates of genetic correlations are in agreement with previous reports (Sorensen *et al.*, 2001; García and Baselga 2002a, b; Abou Khadiga, 2008).

4.3.2. KINDLING INTERVAL

Estimated genetic parameters for kindling interval are presented in Table 11. Kindling interval had low heritability (0.05), low permanent effects (0.05) and low repeatability (0.10).

Similar results to the current results were obtained by Baselga *et al.* (2003) for heritability and repeatability and the value of permanent effects was 0.01. Khalil and Soliman (1989), Moura *et al.* (2001) and Khalil (1993) estimated the heritability of the interval between parities close to zero but in the last study the repeatability agreed with our estimate.

Kindling interval showed negative and low genetic and residual correlations with litter size at weaning (-0.24 and -0.03, respectively) but the environmental permanent correlation was moderate and positive (0.54).

4.4. THE COMPARISONS BETWEEN LINES AT THE ORIGIN

4.4.1. EFFECT OF THE INBREEDING

The different effects of inbreeding levels on litter size traits and kindling interval are presented in Table 12.

The inbreeding had a negative effect on the litter size traits, named inbreeding depression. The inbreeding depression increased with increased inbreeding. At an inbreeding level from 30 to 35% the diminution in total born was 0.66 young, 0.67 in number born alive, 0.67 in number weaned and 0.51 in number marketed. The increase, in the effects, seems non linear. It appears a light effect from the first level ($0 \le F \ge 0.05$), to the second ($0.05 < F \ge 0.10$), a plateau between the third ($0.10 < F \ge 0.15$) and the six ($0.25 < F \ge 0.30$) and a new increase between the six and the seven ($0.30 < F \ge 0.35$).

Table 12: The effect of different levels of inbreeding on litter size (rabbits) and kindling interval (days)

Inbreeding levels	TB	BA	NW	NM	KI
$0 \le F \ge 0.05$	0.00	0.00	0.00	0.00	0.00
$0.05 < F \ge 0.10$	-0.06±0.11	-0.07±0.11	-0.13±0.14	-0.21±0.36	-0.91±0.49
$0.10 < F \ge 0.15$	-0.43±0.14	-0.49±0.14	-0.41±0.17	-0.30±0.45	-2.15±0.61
$0.15 < F \ge 0.20$	-0.33±0.16	-0.28±0.21	-0.28±0.21	-0.27±0.56	-1.97±0.75
$0.20 < F \ge 0.25$	-0.59±0.20	-0.43±0.17	-0.35±0.25	-0.33±0.64	-2.40±0.91
$0.25 < F \ge 0.30$	-0.40±0.22	-0.33±0.23	-0.36±0.28	-0.23±0.75	-3.23±1.03
0.30 < F ≥0.35	-0.66±0.32	-0.69±0.32	-0.67±0.39	-0.51±1.06	-2.19±1.51±

TB: Total born; BA: Number born alive; NW: litter size at weaning; NM: litter size at marketing; KI: kindling interval

Some comments about the standard errors of the estimates of the effects of the inbreeding deserve attention. In general the standard errors were relatively high, particularly for the number marketed, and increased with the level of inbreeding. These high standard errors, despite the high number of records considered in the analysis are an indication that the structure of our data is no well conditioned for the estimation of this effect. One reason could be the relatively close associations between levels of inbreeding and year-seasons (Table 13) and even more with the interaction between farm-year-season effects and inbreeding effects. It is relatively common that the type of data as our have intrinsic difficulties to estimate the effect of the inbreeding (Linch and Walsh,

1998) and to discriminate if the apparent non linearity of the effect is real or a statistical artefact.

The negative inbreeding effects lead to reduce the mean of the traits along the generations, but this reduction does not seem important because the current values of the lines show figures very high, similar o better than the values reported in Spain for commercial farms and different maternal lines (Garreau et al., 2004; Ramón and Rafel, 2002). These lines have been selected successfully for litter size at weaning (García and Baselga, 2002a, b) and the inbreeding depression has not been enough for masking the response to selection. The set of results showed in Table 12 are also indicators of low effects of the inbreeding. The inbreeding negative effects on the litter size traits are in agreement with reports by Ferraz et al. (1991) and Moura et al. (2000) in rabbit and by (Falconer, 1960) in mice. But the reported negative inbreeding effects on litter size traits were higher than in our study. Moura et al. (2000) estimated the reduction in litter size at birth and at weaning caused by a 10% of inbreeding of the doe: 0.81 and 0.59 rabbits per litter, respectively. In the same context, Ferraz et al. (1991) found that the reduction of litter size at weaning can go up to 1.4 rabbits/litter, if the does and litters have inbreeding coefficient of 0.10 and it was the 26% of the trait mean. The inbreeding negative effects on the litter size traits could be a result of reduction in milk production and general maternal ability, as suggested by Brinks and Knapp (1975).

The estimated effects of the inbreeding on the kindling interval seem irrelevant, being the maximum estimated effect -3.23d, that is actually low and is not a depressing effect as it could be expected. All the comments made about the estimation of the effects of the inbreeding on litter size traits apply also to the kindling interval and the overall picture seems to indicate that the effect of the inbreeding on the fertility of our lines was very low.

Group	0-6	7-12	13-18	19-24	25-30	31-36	37-42	43-48	49-54	55-60	61-66	67-72	73-78
Mean	0	0.042	0.031	0.024	0.041	0.069	0.088	0.114	0.134	0.15	0.168	0.177	0.177
Mini	0	0	0	0	0	0	0.1	0.1	0.1	0.1	0.1	0	0
Max	0	0.1	0.1	0.1	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.3	0.067
SD	0	0.015	0.014	0.014	0.025	0.026	0.024	0.027	0.029	0.027	0.023	0.060	0.067
Group	79-84	85-90	91-96	97-102	103-108	109-115	1095	-1100	1101-	1106	1107-	-1112	
Mean	0.146	0.16	0.197	0.173	0.177	0.165	0.0)94	0.1	09	0.1	.24	
Mini	0	0	0	0	0	0	0	.1	0.	1	0	.1	
Max	0.3	0.3	0.3	0.3	0.3	0.3	0	.1	0.	2	0	.2	
SD	0.088	0.082	0.075	0.113	0.118	0.131	0.0)16	0.0	14	0.0)14	

Table 13: Mean, extreme values (minimum, maximum) and standard deviation of the inbreeding by group of farm-year-season level.

4.4.3. CONTRASTS BETWEEN LINES AT THEIR ORIGIN

Table 14 shows the contrasts between A, V, H and LP lines for litter size traits and kindling interval. These contrasts are estimable functions between each couple of lines across the farm-year-seasons common to both. The contrast between the lines H and LP was not possible because they did not share any farm-year-season. The estimated effects needed for the contrasts, line effects and the interaction farm-yearseason-line, came from the analysis that took into account the total set of data, the permanent environmental effects and the additive effects. Because the additive effect of the animals is considered into the model, the response to selection is explained by this effect and, consequently, the effects of the lines in this analysis express the level of them at their origin. Line V, at its origin, was superior to line A (common farm-yearseasons, 9 to 115) in total born, number born alive, litter size at weaning and litter size at marketing, being the difference of 1.33, 1.20, 0.87 and 1.43 rabbits respectively, all of them significant. The contrasts of lines H and LP to line A were significant in favour of line H (common year-seasons, 65 to 96) and line LP (common year-seasons, 95 to 115) for litter size traits. Line LP had litter size traits superior to line V (common yearseasons, 95 to 115). The results showed in Table 14 have some apparent incongruities. For example, the contrast for total born between lines A and V was -1.33 rabbits, between A and LP -1.21 but between V and LP was not 0.12 (1.33-1.21), it was -0.96. The explanation of these non real incongruities comes from the different set of interactions farm-year-season-line involved in the different contrasts. To get a deeper knowledge of the importance of this interaction the Table 15 split the contrasts into two components, the one due to differences between the line effects and the one due to differences between the interactions. Concerning the interactions, some events have happened along the years in the farm at the UPV that explains some of the farm-yearseason-line interactions. The first one was the arrival of the enterocolitis that affected a great part of the period of comparison between the lines A and H (farm-year-season 65-96). The consequence of this disease was an increase in the post-weaning mortality, reducing the number of rabbits marketed. The sensitivity of the lines to the enterocolitis was different, being the line A the line most affected. Consequently this event penalized the line A in all comparisons for number marketed where the period of incidence of the disease was included but particularly the comparison between lines A and H. The comparison between lines A and LP was not affected, because the comparison was made from the farm-year-season 95 to 115. Another event generating an interaction farm-year-season-line was the introduction of new feeders, installed in the cages of line H since the farm-year-season 74 and maintained until the farm-year-season 94. These feeders, in order to avoid wastages of feed, made difficult the access of the does to the feed, diminishing the consumption and penalizing all litter size traits. This explains that a first comparison between the line V and H (Cifre *et al.*, 1998), gave a result favourable to line H but the current comparison did not detect differences between both in total born and number weaned and significant differences in favour of line V for number born alive and number marketed. The third event that has to be commented was a change of the management that affected the lines V and LP during the farm-year-seasons 95 to 102. The change supposed an increase of two weeks of the period of restricted feeding between weaning and the next parity, restriction that affected more to the line V than to the line LP (Theilgaard *et al.*, 2007; Sánchez *et al.*, 2008). The line LP made a better management of feed (Theilgaard *et al.*, 2007).

kindling ir	kindling interval (days)											
Trait	A vs V	A vs H	A vs LP	V vs H	V vs LP							
Total born	-1.33±0.03*	$-1.39\pm0.07^*$	$-1.21\pm0.08^{*}$	0.02±0.08	$-0.96 \pm 0.08^{*}$							
Number born alive	-1.20±0.04*	$-1.06\pm0.08^{*}$	$-1.29\pm0.08^{*}$	$0.28 \pm 0.08^{*}$	-1.32±0.08*							
Number weaned	$-0.87\pm0.04^{*}$	$-0.61\pm0.09^{*}$	$-0.87 \pm 0.10^{*}$	0.11±0.09	$-0.96\pm0.10^{*}$							
Number marketed	-1.43±0.05*	$-2.53\pm0.12^*$	-0.72±0.11*	$0.25 \pm 0.10^{*}$	-0.97±0.11*							
Kindling interval	0.12±0.16	1.44±0.21*	-0.47±0.30	-0.33±0.20	$0.83\pm0.19^{*}$							

Table 14: Contrasts between the lines A, V, H and LP for litter size traits (rabbits) and kindling interval (days)

*: difference significant at $\alpha = 0.05$

At the origin of the lines, the results of Table 14 are showing the superiority of lines V, H and LP over the line A and a simple explanation of these differences comes from the criteria used for their foundation. Lines V, H and LP were created by mating does and bucks of different origins coming from populations that had been submitted previously to selection for prolificacy. The line A was created by mating does and bucks of New Zealand White breed, from a variety of populations more concerned in keeping the standards of the breed than to improve its productivity.

Table 15: Split of the contrasts between the lines A, V, H and LP for litter size trai	ts
(rabbits) and kindling interval (days), in the part due to the line effect and the	ne
part due to the interaction	

Trait	A vs V		A v	A vs H		A vs LP		V vs H		s LP
Tat	L	AE*L	L	AE*L	L	AE*L	L	AE*L	L	AE*L
Total born	-1.22	-0.11	-1.04	-0.35	-1.46	0.25	0.18	-0.17	-0.25	-0.72
Number born alive	-1.06	-0.14	-0.80	-0.26	-1.53	0.24	0.25	0.03	-0.48	-0.84
Number weaned	-0.75	-0.12	-0.56	-0.04	-1.12	0.25	0.18	-0.07	-0.38	-0.58
Number marketed	-1.26	-0.17	-1.49	-1.04	-1.40	0.68	-0.23	0.48	-0.15	-0.82
Kindling interval	0.00	0.12	0.20	1.24	0.04	-0.50	0.20	-0.53	0.04	0.79

L: the line effect; AE*L: interaction farm-year-season-line.

In crossbreeding experiments, analyzing differences in direct effects of the lines, Orengo *et al.* (2003) showed a superiority of line V over line A and Baselga *et al.* (2003) also showed this superiority, but the last authors did not find significant differences between the H line and the lines V and A.

The differences between lines observed for the kindling interval were only significant between the lines A and H in favour of line H and between the lines V and LP in favour of line LP. However these differences were irrelevant, the highest value was 1.44 d. Baselga *et al.* (2003) in the crossbreeding experiment cited before found significant and relevant differences in direct effects for kindling interval between the line A and V (7.4 d), between the line A and H (6.5 d), in favour of lines V and H but not significant between the line H and V (0.81 d), lines that did not show differences between them. Cifre *et al.* (1998) noted that no significant difference between V line and H line (1.02 d) were detected.

4.4.3. THE COMPARISONS BETWEEN LINES AT FIXED TIMES

Table 16 shows the comparisons between the A, V and H lines for litter size traits and kindling interval along the farm-year-seasons 91 to 96. Table 18 shows the same contrasts between the A, V and LP lines during the farm-year-season 110 to 115. The first period allowed the last comparison to line H, because this line moved to another farm at the farm-year-season 96, and the second period allowed the last comparison to line LP that was introduced at the UPV farm, the farm-year-season 95, staying at this farm since this time. These comparisons were made with the exclusive data recorded during the period and did not include into the model the additive effects. Thus, the contrasts between lines were estimates of the real differences between them at the period considered.

Trait	A vs V	A vs H	V vs H
Total born	$-1.85\pm0.16^*$	$-2.30\pm0.21^*$	$-0.45\pm0.21^{*}$
Number born alive	$-1.71\pm0.16^*$	$-1.58\pm0.22^{*}$	0.13±0.22
Number weaned	$-1.02\pm0.14^*$	$-0.58\pm0.18^{*}$	$0.44{\pm}0.18^{*}$
Number marketed	$-1.02\pm0.13^{*}$	$-0.45\pm0.18^{*}$	$0.57 \pm 0.18^{*}$
Kindling interval	$3.71\pm0.62^*$	1.32±0.76	$-2.39\pm0.70^{*}$

Table 16: Contrasts between the lines A, V and H during the farm-year-season 91 to 96 for litter size traits (rabbits) and kindling interval (days)

*: difference significant at $\alpha = 0.05$

Considering the results of the first period, the line H was the best for total born in agreement with the previous results of Cifre et al. (1998), followed by line V, that showed a superiority of 1.85 total born rabbits over line A. A similar superiority was maintained for number born alive (1.71 rabbits) and a little reduced superiority (1.02 rabbits) for number weaned and marketed. However the line H did not maintain the superiority exhibited in total born. Thus, when compared to line V there were no significant differences for number born alive and the differences on number weaned (0.44 rabbits) and number marketed (0.57 rabbits) were significant and in favour of line V. When comparing the line H to the line A, the big superiority of line H in total born (2.30 rabbits), was severely diminished to 1.58 rabbits born alive, 0.58 rabbits weaned and 0.45 marketed. In general the differences that are observed at birth use to be reduced at weaning and marketing time because of the reported positive correlation between litter size at birth and posterior mortalities (Torres, 1986; Szendrő and Barna, 1984; Szendrő et al., 1996), but the severity of this reduction in the comparisons of line H to lines A and V needs a more thorough explanation. The explanation is the same that was invoked to explain some incongruities in the previous section. It was the change of the feeders in the cages of line H during the farm-year-seasons 74 to 94, that penalizes total born, but more number born alive and more number weaned and marketed. Concerning kindling interval the differences were significant between line V and the line A (3.71 d) and line H (2.39 d) in favour of line V. The difference between line A and H was non significant. The maximum difference observed, 3.71 d is relatively important, because it is around 7.5% of a normal kindling interval of 49 d.

The observed difference between A, V and H lines during the farm- year-season 91 to 96 can be compared with the expected differences computed with the results of the analysis used to make the comparisons at the origin of the lines. The expected differences are computed as the contrasts between the lines during the farm-year-season 91 to 96 plus the difference between the averages of the additive values of the animals of each line having litters in the period, weighed by the number of litters. The expected differences are in the Table 17, which shows values very similar to the observed differences reported in the Table 16. This similarity could be considered as an indicator of the goodness of the models used to analyse the traits.

Table 17: Expected contrasts between the lines A, V and H during the farm-year-season 91 to 96 for litter size traits (rabbits) and kindling interval (days)

Trait	A vs V	A vs H	V vs H
Total born	-1.83	-2.14	-0.30
Number born alive	-1.67	-1.11	0.56
Number weaned	-0.96	-0.21	0.75
Number marketed	-0.91	-0.14	0.77
Kindling interval	3.39	1.06	-2.34

The comparisons during the farm-year-seasons 110 to 115 (Table 18), between the lines A, V and LP show a very different picture between the lines A and V to the one showed during the period from the farm-year- season 91 to 96 (Table 16). The big superiority exhibited by the line V compared to line A was severely reduced for all litter size traits. The difference of 1.85 total born rabbits was reduced to 0.48, that was significant, but the differences for number born alive, number marketed and kindling interval became non significant.

The contrasts, between the line LP and the lines V and A, were not significant for any trait. As a summary of the results of this comparison it seems that the lines A, V and LP show currently similar performances in reproduction. If the absolute values of the analyzed traits were taken into account the more important result would be the big improvement achieved by the line A.

We can compute the expected differences between the lines during the farmyear-season 110 to 115 (Table 19), as we have explained above, and compare with the observed differences /Table 18). As occurred in the comparison during the periods 91 to 96, in this comparison was observed, again, a high similarity between both types of comparisons for litter size traits. For kindling intervals the similarity was lower between the observed and expected differences especially between A and LP lines and between V and LP lines. However the relevance of the discrepancy is low.

Table 18: Contrasts between the lines A, V and LP during the farm-year-seasons 110 to115 for litter size traits (rabbits) and kindling interval (days)

Trait	A vs V	A vs LP	V vs LP
Total born	$-0.48\pm0.17^{*}$	-0.21±0.16	0.27±0.16
Number born alive	-0.15±0.18	-0.24±0.17	-0.10±0.17
Number weaned	-0.04±0.15	-0.03±0.13	0.01±0.13
Number marketed	-0.22±0.15	-0.24±0.13	-0.02±0.13
Kindling interval	0.56±0.71	0.69 ± 0.70	0.13±0.65

*: difference significant at $\alpha = 0.05$

Table 19: Expected contrasts between the lines A, V and LP during the farm-yearseasons 110 to 115 for litter size traits (rabbits) and kindling interval (days)

Trait	A vs V	A vs LP	V vs LP
Total born	-0.49	-0.20	0.29
Number born alive	-0.10	-0.15	-0.05
Number weaned	-0.03	0.02	0.04
Number marketed	-0.20	-0.21	-0.01
Kindling interval	0.79	2.34	1.55

5. CONCLUSIONS

From the current results it could be concluded that:

- 1. Some practices in mating and selection management allow and increase of the inbreeding coefficient lower than 0.01 per generation in maternal lines of around 25 males and 125 females, selected for litter size at weaning.
- The heritability of litter size traits was low (0.08-0.14) and even lower for kindling interval (0.05). The repeatability of these traits was low-moderate (0.10-0.25). The genetic correlation between litter size at weaning and the other litter size was high and positive (0.80-0.94). However, the genetic correlation between litter size at weaning and kindling interval was negative, but low (-0.24).
- 3. The structure of the data coming from programmes of selection is no well conditioned for the estimation of the effect of inbreeding. A low inbreeding depression was detected for litter size traits. The inbreeding had an irrelevant effect on kindling interval (fertility).
- 4. There are interactions between farm-year-season and lines that modulate the comparisons between the lines.
- 5. Important differences have been detected between the lines at their origin that could be explained by the criteria used for the foundation.
- 6. A high agreement has been observed between the observed differences of the lines at fixed times and the expected differences derived from the selection and models used for the traits. This similarity could be considered as an indicator of the goodness of these models.
- 7. The current performance of the lines is much closer that at their origin. The reproductive performance of the four maternal lines (A, V, H and LP) is high and they appear as competitive lines to produce crossbred does.

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