

GENETIC IMPROVEMENT OF MEAT RABBITS. PROGRAMMES AND DIFFUSION

BASELGA M.

Departamento de Ciencia Animal. Universidad Politécnica de Valencia. Camino de Vera,
14. 46071 Valencia. Spain. mbaselga@dca.upv.es

ABSTRACT

The essential elements of a programme of genetic improvement of meat rabbits, required to satisfy the needs of animals demanded by the producers of rabbit meat in a region or country, are analysed. The three way crossbreeding scheme is adopted to discuss the programmes. In this context, the development of maternal and paternal lines is one of the central points and a historical enumeration of research or development centres involved in this activity is presented. The principal criteria in founding new lines are discussed and the interest is noted in finding two or three populations, no matter their genetic origin (pure breed, synthetics or crossbred), that are clearly outstanding for the traits important to the desired specialisation of the line. The alternative of applying very high intensities of selection for the traits of interest in very large populations is also commented upon (for example, commercial populations made up by a large number of farms) and examples of founding a line following criteria of hyperprolificacy and another of hyperlongevity are given. Paternal lines are commonly selected for post-weaning daily gain or weight at time of marketing by individual selection. The most common criterion used to select maternal lines is litter size at birth or at weaning, but there are proposals to include traits related with the ability of the doe to nourish the lactating progeny, traits such as weight at weaning, litter weight at weaning or total milk production. Currently, mixed model methodology (BLUP) is the habitual procedure used to evaluate the animals genetically, using repeatability animal models for litter size and selecting the progeny from the best evaluated matings. The responses reported in paternal lines range between 18 and 35 g/generation for weight at market time and between 0.45-1.23 g/d. generation for daily gain, with correlated responses increasing adult weight, intestinal content and feed intake but decreasing feed conversion, dressing percentage and maturity at a fixed weight. The responses estimated in maternal lines range between 0.05-0.13 rabbits born alive or weaned per litter and generation, figures 0.08-0.09 being common. Depending on the lines, ovulation rate or foetal survival were the modified components that explain the responses in litter size. Comparing the responses in crossbreeds with the responses in pure lines, slightly higher responses were obtained for the crossbred does; however, the response was lower than expected for the young issued from the terminal mating, probably due to an interaction between the feed currently used to control enterocolitis and the genetic level for growth traits. Finally, two approaches to diffuse the genetic improvement to the producer are presented which modify the standard pyramid of selection, multiplication and production, aiming to increase the selection effort and minimise the genetic lag between selection and production.

Key Words: selection, lines, response, programs, diffusion

INTRODUCTION

The main objective of this paper is to analyse the essential elements of a programme of genetic improvement of meat rabbits in order to satisfy the needs of animals required by the producers of rabbit meat in a region or country. Until now, there have been only a few programmes with this orientation and some of them provide animals to their own country as well as abroad. Nevertheless, many countries are attempting to develop full or partial programmes and for them some discussion about the principal guidelines would be useful, such as the minimum facilities needed, the requirements to be fulfilled and what the expected responses from the programmes are. The final aim of this analysis is to try to encourage people involved in the initial stages of this activity to go ahead, because the rabbit is reared under very different environmental conditions, types of feeding and systems of management that require genetic selection to be carried out under their peculiar local conditions.

First, the interest of crossbreeding in rabbit production is discussed, in order to understand that the development of maternal and paternal lines is the crucial point of a genetic improvement programme. Then, different items related with the development of lines, such as criteria for their founding, selection methods and criteria, expected responses in purebreeding and crossbreeding are addressed. Finally, two ways to diffuse the genetic improvement to the farmers will be dealt with, differing in the size of the companies involved in the diffusion, the scope of their trade - regional, national or international - and the running costs.

CROSSBREEDING AND RABBIT PRODUCTION

Intensive meat production in rabbits is based on a three-way crossbreeding scheme. A first cross involves two maternal lines generating crossbred does. A second cross consists of mating males of a third line, commonly selected for growth rate or weight at a given age, with the crossbred does to produce the rabbits to be slaughtered for meat. The aim of 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. 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. In France, since the seventies, the INRA (SAGA, Toulouse) has been selecting two maternal lines for litter size traits. These lines, named A2066 and A1077, were crossed to obtain the crossbred doe 1067. In 1994, BRUN and SALEIL (1994) gave estimates of the heterosis for the cross of these lines. The estimates were 15.2%, 20.1% and 6.7% for the traits total litter size, born alive and number of young weaned, the experiment being carried out in farm conditions. This explains the low value of heterosis for number of weaned rabbits because of the practice of some farmers of taking out some young at birth. These figures are important, despite the long number of generations of selection followed in those lines. NOFAL *et al.* (1996) gave values of 12.5%, 10.0% and 5.5% of

heterosis for the same traits previously cited for the cross between New Zealand White and Californian. The heterosis between line V (maternal lines, UPV, Spain) and A2066 for the traits total litter size and number born alive was studied by BRUN *et al.* (1998), reporting values of 13.6% and 20.7% for these traits. In Spain, there are two public centres that join their efforts in developing a programme of rabbit genetic improvement. These centres are the Department of Animal Science (UPV, Valencia), and the Rabbit Science Unit (IRTA, Barcelona). Recently (BASELGA *et al.*, 2003), the crosses between maternal lines of the UPV (lines A, V and H) were studied. Line A showed significant individual heterosis with lines V and H in prolificacy traits, total born and live born per litter. Heterosis estimates ranged between 0.45 and 0.98 young per litter (4 and 10%). No significant heterosis, for any trait, was detected between lines V and H. ORENGO *et al.* (2003) have studied the cross between the lines A, V and Prat (IRTA, Spain) finding individual heterosis for litter size traits ranging between 7 and 16%.

In the terminal cross, between the crossbred doe and the paternal line, complementarity plays a central role in the sense that the aim is that the crossbred doe should be extreme as regards reproductive performance and the paternal line as extreme as possible in growth, feed efficiency and carcass traits.

DEVELOPMENT OF LINES

In this context, the development of maternal and paternal lines is a crucial activity. We have already mentioned the involvement of the INRA in France, and the UPV and IRTA in Spain, developing lines to be used in crosses. The French programme has its roots in 1961 when the control of performance in farms began (BANEYE, 1975; ROUVIER, 1975), but it was in 1969 when the organisation to produce paternal and maternal lines was decided upon (ROUVIER, 1981). The work of development of lines started in Spain at UPV and IRTA in 1976. The French and Spanish programmes have kept their work uninterrupted until now and all the lines created in the beginning have undergone more than thirty generations of selection. There are other examples of public institutions in other countries developing rabbits lines for use in production. In the U.S.A., in 1988 the Alabama A&M University began the selection of a paternal line that has continued since 1994 in the Texas A&M University (Department of Animal and Wildlife Sciences, line Altex). In Hungary, since 1991, the faculty of Animal Science (Pannon University of Agriculture, has been developing the White Pannon Breed, selected for growth rate (GARREAU *et al.*, 2000). In Uruguay, the INIA (Las Brujas, Canelones) has had a programme since 1999 involving two maternal and one paternal lines (CAPRA *et al.*, 2000). In Egypt, great efforts have been made since 1998 to select one exotic maternal line under their local conditions and to develop and select local lines based partially on local breeds. The Faculty of Agriculture of Alexandria (Department of Poultry Production), the Animal Production Research Institute (APRI, Cairo) and the Faculty of Agriculture of Moshtohor (Department of Animal Production) are involved in this Egyptian programme. In Saudi Arabia, since 2000, a programme is being developed at King Saud University (Department of Animal Production and Breeding, Buriedah) that has high similarities to the Egyptian. In Mexico, the first global attempt to develop a programme was in 1976 in the Centro Nacional Cunicola de Irapuato assisted by the INRA (PÁEZ CAMPOS *et al.*, 1980) and now the Colegio de Postgraduados (Montecillo)

and the Facultad de Altos Estudios Cuautitlán (UNAM, México) are engaged in active work developing and selecting rabbit lines.

Criteria to found new lines

The most common practice in the past was to rely on the existing breeds and to get samples of one or several of them (LUKEFAHR *et al.*, 1996) to create a new population of small size that after two or three generations of inter-se mating gives rise to the new line (KHALIL AND BASELGA, 2002). The final size of the line can range between 100-200 does and 20-40 bucks. This procedure is not difficult to carry out but care must be taken because some problems can arise. One problem comes from the enormous diversity that can exist within a breed. This means that you may sample the founder stock for the new line from populations of the breed that are genetically poor for the traits of interest and consequently the starting point for the new line will be low and possibly non-competitive. Another setback could be health problems that could appear when all the founders are put together in the same herd but come from a relatively large number of different farms. This latter problem can be overcome by using hysterectomy or other techniques such as freezing and transfer of embryos to obtain animals from the farms (GARCÍA-XIMÉNEZ *et al.*, 1996).

Now, we comment on two alternatives to the described procedure to found lines. In both cases, the first point is to define realistically the desired specialisation of the line. The first alternative attempts to find two or three populations, no matter their genetic origin (pure breed, synthetics or crossbred), that are clearly outstanding for the traits important to the desired specialisation of the line (BASELGA, 2002). The next step is to obtain animals from these populations and mate them without selection for two or three generations. The second alternative relies on applying very high intensities of selection for the traits of interest in very large populations (for example, commercial populations). We illustrate this procedure detailing the foundation of line H (UPV, Spain). It is based on the detection of does named hyperprolific, screening a large population of commercial rabbits, spread over different Spanish farms. A doe was sorted as hyperprolific if it had a parity with 17 or more young born alive or if her accumulated number of live born along all its parities allowed its classification in the group of the best 1%. An initial step in the process was to obtain male progeny from a batch of hyperprolific does (20) mated to normal bucks (9 bucks, pertaining to line V). In the second step, the males obtained in the first step were back-crossed to a new and larger batch of hyperprolific females, in order to accumulate the genes for prolificacy in the progeny. The progeny obtained was the starting generation of line H (*generation 0*). In this alternative, the health problems could be important and to avoid them hysterectomies were performed in the first step and embryo vitrification in the second step. After thawing and transferring these embryos, a set of 474 rabbits of generation 0 were allowable for maintaining the line and for studies of comparison of the line H with the line V and crossbred does AxV. Comparison was successful for line H (CIFRE *et al.*, 1998 a, b). After three generations without selection, we started the selection for number born alive per litter. The same alternative is being applied to create a new line for which the criteria of screening in the commercial farms are hyperlongevity, and prolificacy over the mean (UPV, Spain). In this case, two steps of backcrosses have been performed.

Criteria and methods of selection

It is necessary to distinguish according to the specialisation of the lines, paternal or maternal. Paternal lines are commonly selected for post-weaning daily gain (ROCHAMBEAU *et al.*, 1989; ESTANY *et al.*, 1992; GÓMEZ *et al.*, 2002) or for a weight at a time close to the market age (LUKEFAHR *et al.*, 1996; LARZUL *et al.*, 2003a). These criteria are very easy to record and have a negative and favourable genetic correlation with the conversion index (MOURA *et al.*, 1997; PILES *et al.*, 2004) which is very important for an efficient production. The conversion index is not used directly because is expensive to record and would need, when collective cages are used, complex electronic devices to enable recording of the individual feed intake. If fattening is done in cages, housing only one rabbit, control of the feed consumption could be manual but, anyway, is also expensive and there could be a genotype type of cage interaction. The methodology used to select these traits has been, in general, individual selection. It is the simplest procedure and is possible because the traits are expressed in both sexes and the heritability is medium. In this way we can save time, labour and resources. The interval between generations could be around six months. SZENDRO *et al.* (1996) attempted to select the White Pannon breed for daily gain and carcass quality, assessed by the average surface of *longissimus dorsi* using computerised tomography. In the future, in lines highly selected for growth, a close connection between the nucleus of selection and the artificial insemination centres will allow semen and other adult male traits to be included in the criteria and objectives of selection.

Regarding selection of maternal lines, the situation is more complex. Here we shall comment on only the most common approaches because GARREAU *et al.* (2004) review in this congress the current situation, the future and experimental alternatives for the selection of maternal lines. The most common criteria of their selection have been related with litter size at birth or at weaning (ESTANY *et al.*, 1989; GARREAU *et al.*, 1994; GÓMEZ *et al.*, 1996). In one case, the selection criteria include litter size at birth and weight at nine weeks to prevent negative responses in adult weight (BOLET and SALEIL, 2002) and there are proposals for the selection of these lines 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.

Selection methods in maternal lines are more complicated than in sire lines. This complexity is due to the fact that males do not express the litter size traits themselves and to the low values of the heritabilities of reproduction traits. So, it is necessary to consider as many own and relative records as possible in the genetic evaluation of does and bucks. In addition, the generation interval is longer than in the selection of sire lines and, consequently, it could be necessary to take into account some environmental and physiological effects in the models of evaluation (ARMERO *et al.*, 1996). Family indexes were proposed to integrate the own information and the information of the relatives to carry out the genetic evaluation (MATHERON and ROUVIER, 1977; BASELGA *et al.*, 1984). This methodology is still applied for the selection of line A (UPV, Spain) that is in the 32nd generation of selection. In this case, the evaluation of a doe or buck is by a family index that has a maximum of four items: average litter sizes at weaning of the individual

to be evaluated if it is a doe, of its dam, full sisters and half (paternal or maternal) sisters.

Currently, mixed model methodology (BLUP) is the procedure most used in evaluation. One of the biggest differences with the family index is that some environmental and physiological effects are considered in the model (ESTANY *et al.*, 1989; GÓMEZ *et al.* 1996; ROCHAMBEAU *et al.* 1998). Simulation studies with real data have shown similar efficiencies of both methodologies for selecting litter size. The loss of response due to selection on a family Index instead of a BLUP is around 8% (ARMERO *et al.*, 1996) when the generations of selection do not overlap. All these methods of selection increase the inbreeding of the lines generation after generation and it is necessary to manage the lines in an attempt to minimise the losses of genetic variability. This aspect is analysed by KERRILES AND ROCHAMBEAU (2002) along 20 generations of selection of the maternal INRA lines.

Within line responses

The standard way of estimating the response in selection experiments has been the use of a control population that is developed parallel to the selected population but without carrying out selection. Another common method is divergent selection, studying the differences between two lines selected contemporarily, one to increase a trait and another to decrease it (SANTACREU *et al.*, 2000). The use of frozen embryos (SANTACREU *et al.*, 2000) allows the contemporary comparison of two different generations of the same line. After the development of different reproductive techniques, its use is considered to estimate responses to selection. All these methods are neither model dependent nor dependent on the genetic parameters of the traits. There are statistical methods, such as mixed model methodology (BLUP and REML) and Bayesian Inference, that are used to estimate genetic trends or responses to selection that are dependent on the models, the parameters and the information used "a priori". These statistical methods have been applied in rabbits. There are experiments that were analysed at the same time by both types of methods. In many cases there was a good agreement between the responses estimated by both types of approaches, but not always. The consequence is that the statistical methods need some type of previous validation in the populations and traits under analysis before their use to estimate response to selection.

The responses reported in experiments of selection for weight at market time, 63-70d, range between 18 and 35 g per generation (ROCHAMBEAU *et al.*, 1994; LUKEFAHR *et al.*, 1996; GARREAU *et al.*, 2000; LARZUL *et al.*, 2003a) and there is a good agreement between the estimates of the responses obtained using control line or mixed model methods (LUKEFAHR *et al.*, 1996; LARZUL *et al.*, 2003a). When selection was for growth rate, the responses were between 0.45 and 1.23 g/d (ROCHAMBEAU *et al.*, 1989; ESTANY *et al.*, 1992; PILES and BLASCO, 2003). In the experiment of PILES and BLASCO (2003), the response was estimated using frozen embryos and by Bayesian Inference and both methods gave the same estimate. There are correlated responses to selection for growth as an increase in the adult weight (BLASCO *et al.*, 2003). At a fixed slaughter

weight, the feed conversion decreases and feed consumption increases (FEKI *et al.*, 1996); intestinal content increases, and the dressing percentage is reduced (GÓMEZ *et al.*, 1998; PLA *et al.*, 1998) because of the lower maturity. Consequences of this lower maturity are also reduced fat deposits, diminished water holding capacity of the meat (PILES *et al.*, 2000) and lower ultimate pH in muscle (GONDRET *et al.*, 2033). Some of the negative consequences of selection for growth rate are not quantitatively important and can be reduced by increasing the market weight and imposing a light fasting before slaughter. In an analysis at a constant age, the improvement in the conversion index can disappear as well as the negative effects on dressing percentage and maturity (GARREAU *et al.*, 2000; LARZUL *et al.*, 2003b).

Regarding the response to selection in maternal lines, we are to comment only on the reported results concerning lines involved directly in rabbit breeding programmes because, as mentioned previously, a more complete analysis, including lines of interest in production or otherwise, is done in another paper of this Congress (GARREAU *et al.*, 2004). 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, 2002 a, b), estimate responses to selection between 0.08 and 0.09 rabbits total born, born alive or weaned per litter and generation. In the same lines, the responses estimated, as genetic trends, by mixed model methods (BLUP and REML) completely agree in the first three experiments (ROCHAMBEAU *et al.*, 1998; GARCÍA and BASELGA, 2002 a; TUDELA *et al.*, 2003), but the genetic trend estimated in the fourth is 0.175 weaned rabbits per litter and generation, a figure approximately double that of the response estimated using frozen embryos. There are also reports of responses estimated exclusively by mixed model methods, the estimates ranging between 0.05 and 0.129 live born or weaned rabbits per litter and generation (ESTANY *et al.*, 1989; ROCHAMBEAU *et al.*, 1994; GÓMEZ *et al.*, 1996). In some of these lines with significant responses in litter size, studies have been carried out to ascertain whether some component of the litter size had been modified. GARCÍA and BASELGA (2002 a) found that the main explanation of the response in litter size was the improvement in ovulation rate but in another line (GARCÍA and BASELGA, 2002 b) found that foetal survival was probably the trait actually improved that could explain the observed response in litter size. The correlated responses in growth traits when selection is for litter size have also been investigated. BASELGA and GARCÍA (2002) and GARCÍA and BASELGA (2002 c) did not find significant responses for weight at weaning, weight at market time, post-weaning daily gain, daily feed intake and conversion index, when the comparisons were done at a constant litter size at birth. However, ROCHAMBEAU *et al.* (1994) reported that selection for increased litter size resulted in a decrease of individual weight at weaning but the total weight of the litter at weaning increased in two different maternal lines. This consideration has meant the modification of the selection objective in one maternal line, including in the objective the weight at 63 days, in addition to litter size performances (ROCHAMBEAU, 1998) attempting to increase litter size and individual weight at the same time.

Crossbred responses

It has been mentioned before that the final aim of the genetic improvement of the lines is the improvement of the performance of the crossbred doe and crossbred young. However, no matter which lines are used in crossbreeding, their selection, such as has been presented, is on a within-line basis expecting that the response will also be expressed in the crosses. In this sense, it is crucial to evaluate the response of the selection programmes on the crossbred doe and young.

The French programme was concerned about the evolution of the parameters of the cross between the maternal lines through time and from time to time carried out experiments with the aim of estimating these parameters (direct and maternal additive and heterosis effects). The conclusions are not clear. It seems that between the first experiment in 1970 and the second in 1979, the estimates were different and not predictable in advance (ROUVIER and BRUN, 1990). Nevertheless, comparing results of the heterosis of the third experiment in station and an almost contemporary experiment in commercial farms the estimates were remarkably the same for total litter size and number born alive, but lower in farms than in station for litter size at weaning, as commented before (BRUN and SALEIL, 1994).

The analysis of the parameters of the cross through time enables us to understand the differences between the lines and the crossbreeds, but not the differences between the lines and between the crossbreeds over time, because to do so it is necessary to carry out contemporary comparison among animals (pure or crossbred) representing different stages of the programmes. Such a comparison was made by TUDELA *et al.* (2003) and COSTA *et al.* (2004). The maternal lines involved in the first experiment were the A1007 at the 30th generation of selection and the control A9077 both crossed to a second French maternal line at its current generation. The difference in total litter size between both types of crossbred does was 1.43, a little higher than the expectation from selection of the line A1077 (1.12). In the second experiment the maternal lines were A and V, the A at two different generations of selection. In this experiment the crossbred does came from mating does of the V line to bucks of the A line. The young were the progeny of the cross between the crossbred does and bucks of the R line. Two types of crossbred animals, hereafter called H1 and H2, were compared. The H1(H2) does came from the cross of bucks of generation 16 (29) of line A with females of generation 26 of line V. The young H₁(H₂) were obtained by mating does H1(H2) to bucks of generation 6(18) of line R. The old generations were conserved as frozen embryos and thawed and transferred to produce adults contemporary to the current generations. All the responses in litter size and daily gain were in favour of the current crossbreeds. Concerning litter size traits the differences were 0.83, 1.16 and 0.74 respectively for total litter size, number born alive and number at weaning. These responses were higher than expected from the responses evaluated in the pure lines. For example, the expected response in litter size at weaning was 0.55. In contrast, the responses in the crossbred young were lower than expected. The response for post-weaning daily gain was 0.6 g/d although the expected response was 2.4 g/d. No responses were obtained for daily feed intake and conversion index but the consumption was expected to increase and the conversion index decrease. The authors have no explanation for these results, concerning growth

traits, and suggest that they could be a consequence of the type of feed currently used to control a new disease, spread all over Europe, called epizootic enterocolitis, that can have different effects on the growth of the animals depending on the genetic type source.

DIFFUSION OF THE GENETIC IMPROVEMENT

The final step of a programme is to diffuse the achieved improvement from the nucleus to the farms. The standard way is to follow a pyramidal organisation, including the multiplication of the nucleus stock, as an intermediate step, before the commercial farms. At the multiplication stage, the cross between maternal lines is finally done and the crossbred does are supplied to the farmers, but this step can be preceded by a multiplication of the pure lines. In this way, the costs of selection are spread to a higher number of animals. The genetic lag between the nucleus and the farms increases as the stages of multiplication increase. In order to minimise the lag, the French and Spanish programmes have modified the standard of multiplying the stock converting the intermediate stage of multiplication of the pure lines in a true stage of selection. The French programme does so through what is called “demultiplication”, contracting with some companies the breeding of the maternal lines. On the “demultiplication” farms, the does are selected as in the nucleus but the bucks are supplied by the nucleus. The companies that “demultiply” can be big companies aiming to sell pure or crossbred stock throughout France and other countries (Rochambeau, 1998). In France, three private companies are involved in the meat rabbit genetic improvement. They have created and selected their own male and female lines. One of these companies is involved in the “demultiplication” scheme. The Spanish approach is slightly different, and completely integrates the multiplication of the maternal lines and their selection. The chosen way is to create what could be called secondary nuclei of selection, owned by farmers, co-operatives or small companies. One maternal line is replicated in each secondary nucleus and is selected, under the responsibility of the geneticists of the primary nucleus, in the same way as in the latter. The line selected in the secondary nucleus is used as the dam to produce crossbred does that are commonly distributed to, or produced by, the farmers of the region near the secondary nucleus. The sires to get the crossbred doe, pertaining to another maternal line, are supplied by the primary nucleus. The main feature of this approach is its simplicity, allowing to produce pure line stock and crossbred does at very low prices with a minimum lag between breeders and producers. This approach reduces the health and adaptation problems deriving from the introduction of foreign animals into the farms and improves the communication between breeding companies and farmers. The main disadvantage is the difficulty of operating on a large scale.

The diffusion of the paternal line bucks for the terminal cross can have more different modalities. The paternal lines can be owned and selected by the “demultipliers”, by the secondary nucleus, by the primary nucleus or by breeders not related to the programme, associated or not to artificial insemination centres. It is very common in the Spanish programme that the secondary nuclei have their own artificial insemination centre,

facilitating in this way the complete diffusion of the animals involved in the double cross. In France, breeding companies are also involved in artificial insemination centres.

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