

METHODS, CRITERIA, TECHNIQUES AND GENETIC RESPONSES FOR RABBIT SELECTION: A REVIEW

Khalil M.H.*, Al-Saef A.M.

College of Agriculture and Veterinary Medicine, Qassim University, Buriedah 51452, P.O. Box 6622, Saudi Arabia.

*Corresponding author: maherhkhalil@yahoo.com

ABSTRACT

Based on an extensive review of the literature, the most common selection criteria used in selection programs for maternal lines were related to litter size at birth or at weaning, while in other cases selection programs were practiced for litter size at birth and weight at nine weeks, number of teats, traits related to the ability of the doe to lactate and nourish the progeny (e.g., weight at weaning, litter weight at weaning or total milk production), and in few cases selection for hyperprolificacy and longevity have been introduced recently. Selection for ovulation rate and uterine capacity using new reproductive techniques has been successfully performed, which can be used as an alternative to improve litter size and prenatal survival. For paternal lines, post-weaning daily gain or marketing weight are commonly selected on individual basis. New techniques, such as laparoscopy, ovariectomization, cryopreservation of embryos and semen, TOBEC (Total Body Electrical Conductivity) and X-ray scanning computerized tomography (CT), were used as tools to assist in selection programs. The application of molecular techniques in selection of rabbits so far has had a limited impact on farm animals. Major genes with large effects on litter size components have been identified. Family index or BLUP are the common procedures used to evaluate the animals genetically in selection experiments. Canalization selection model was recently used in evaluation of does and bucks in selection experiments and this model incorporated the classical genetic effects acting on the mean production level, in addition to the other genetic effects acting on the residual variance. Several synthetic maternal, paternal and multi-purpose lines were developed using different criteria and methods of selection. Selection responses were estimated commonly by regressing the estimates of the breeding values on the generation's number, or by using the control populations or the population selected divergently, or by comparing the contemporaries of two different generations using the frozen embryos of the same line. Selection responses obtained in crossbred rabbits could be periodically evaluated by estimating the crossbreeding parameters in the cross (e.g., direct and maternal additive, direct and maternal heterosis, recombination effects, etc.), or by comparing heterosis values obtained from an experiment with those of contemporary commercial farms, or by evaluating the selection responses at different stages of the programme by carrying out contemporary comparisons among purebred and crossbreds.

Studies that have compared selection responses in crossbreds with the responses in pure lines, have observed slightly higher responses in the crossbreds. Direct selection responses per generation estimated for litter size born or weaned were low or slightly moderate and ranged from 0.081 to 0.180 rabbits, while the correlated responses ranged from 0.03 to 0.18 ova for ovulation rate, and 2.0 to 3.7% for prenatal survival. Depending on modified components of litter size, selection for uterine capacity produced responses that were similar to that obtained in direct selection for litter size. Improvement in litter size caused by selection for uterine capacity was not greater than the improvement obtained from direct selection for litter size (approximately 0.1 rabbits per litter per generation). Does selected for litter size at weaning presented significant responses in feed intake (3%) and milk yield (6%). A response of 62 g per litter was recorded when selecting for litter weight at weaning, with a correlated response of 0.17 rabbits for litter size born and weaned. Estimates of direct selection responses per generation were moderate and ranged from 8.7 to 12.6 g for weaning weight, 18 to 68 g for marketing weight, 0.45 to 1.73 g/d for weight gain from weaning to marketing, and 0.05 to 0.27 g feed per g gain for feed conversion from weaning to marketing, which was associated with an increase in correlated responses in adult weight and feed consumption, but with decreasing rate in feed conversion. Selection for growth rate has little or somewhat moderate effects on carcass characteristics and meat quality

when rabbits were selected at the same stage of maturity, which was associated with increases in intestinal content and decreases in dressing out percentage and fat deposits, and ultimately in pH in muscle and water holding capacity of the meat. Selection for litter weight at weaning achieved considerable responses in growth rate with maintaining high litter components and feed conversion. By selection, total fleece weight increased significantly associated with correlated improvements in live body weight and fleece qualities (bristle length and diameter, follicle ratios, compression, resilience, and fibre diameter). Selection responses estimated by different methods were in good agreement to most studies reviewed.

Key words: Selection, Methods, Criteria, Techniques, Responses, Synthetic lines, Rabbit.

INTRODUCTION

Long-term selection experiments carried out in rabbits for more than 10 generations throughout the world were few compared to the major species of livestock (Baselga *et al.*, 1992; Rochambeau *et al.*, 1994, 1998; Lukefahr *et al.*, 1996; Gómez *et al.*, 2000; García and Baselga, 2002a, 2002b, 2002c; Blasco *et al.*, 2005; Khalil *et al.*, 2005). However, selection for productivity in rabbits has been performed in three directions: (1) to improve prolificacy and lactation (maternal lines), (2) to improve growth rate and carcass and meat quality traits (paternal lines) and (3) to improve total litter traits and growth traits together (multi-purpose lines). In the first case, selection was practiced mainly for litter size at birth or weaning, while in the second case the weight gain and/or carcass traits were regarded as the most important selection criteria, and the third case dealing with selection for litter size, litter weight, milk yield, and post weaning growth traits. As a result of selection, some synthetic maternal lines were developed in France (INRA2066, INRA2666 and INRA1777), in Spain (lines A, V, PRAT, H and LP), in Saudi Arabia, (line Saudi-2), in Egypt (line APRI) and in Uruguay (line NZW and V), while the synthetic paternal lines developed were line R in Spain, Altex in USA, White Pannon in Hungary, Alexandria in Egypt, and Saudi-3 in Saudi Arabia. But, the synthetic multi-purpose lines developed were INRA1077 in France, Caldes in Spain, Botucatu in Brazil and Moshtohor in Egypt.

In selection experiments, several methodologies have been proposed to estimate selection responses. One of them was based on the estimates of the breeding values on generations and this approach depends on the genetic parameters and the model used (Estany *et al.*, 1992; Sorensen and Johanson, 1992; Garreau *et al.*, 2000; Gómez *et al.*, 2000; Moura *et al.*, 2001; Ibañez *et al.*, 2006). The other methodologies do not depend on the genetic parameters and the model itself, but are dependent on another approach through use of a control population, which could be an unselected population (Rochambeau *et al.*, 1989, 1994, 1998; Lukefahr *et al.*, 1996; Sánchez *et al.*, 2004b), or using the population selected divergently (Moura *et al.*, 1997; Gondret *et al.*, 2002; Blasco *et al.*, 2005; Mocé *et al.*, 2005; Santacreu *et al.*, 2005; Rafat *et al.*, 2007, 2008) or using the cryopreserved populations that are free of genetic drift to compare the contemporaries of two different generations (Santacreu *et al.*, 2000; Baselga and García, 2002; García and Baselga, 2002a, 2002b, 2002c; Blasco *et al.*, 2003; Piles and Blasco, 2003; Gil *et al.*, 2006).

Molecular technologies were recently used to identify the genetic diversity, gene mapping and DNA fingerprinting (Bolet *et al.*, 2000; Van Haeringen *et al.*, 2001, 2002; Korstanje *et al.*, 2003; Sacharczuk *et al.*, 2005; Chantry-Darmon *et al.*, 2006). But, the results of QTL analysis for productive and reproductive traits are not sufficiently available to be used in selection programs.

The main objectives of this article are concentrated in dealing with reviewing, generalising, and evaluating the selection experiments carried out in rabbits in some parts of the world for productive and reproductive traits in terms of: (1) methodologies used in selection; (2) criteria and techniques assisted in selection programs; (3) application of molecular techniques in selection; (4) estimation of direct and correlated selection responses; (5) programs of selection performed in breeds and those used to develop new synthetic lines.

METHODOLOGIES USED IN SELECTION

Methods applied in selection programs

Selection methods used to develop new synthetic lines of rabbits are more complicated for maternal lines than for paternal lines. This complexity is due to the fact that litter size traits are not expressed in both sexes and to the low values of heritabilities for reproductive traits (Baselga, 2004). So, it is necessary to consider as many individual and relative records as possible in the genetic evaluation of does and bucks. In addition, the generation interval for selection in maternal lines is longer than in selection of paternal lines and, consequently, it could be necessary to take into account some environmental and physiological effects in the models of evaluation (Armero *et al.*, 1995; Baselga and García, 2002; García and Baselga, 2002a, 2002b, 2002c).

The BLUP procedure was the most common procedure used in evaluation of does and bucks in selection experiments in rabbits (e.g. Estany *et al.*, 1989, 1992; García-Ximenez *et al.*, 1996; Gómez *et al.*, 1996, 2000, 2002b; Moura *et al.*, 1997; Rochambeau *et al.*, 1998; Szendrő *et al.*, 1998; Bolet and Saleil, 2002; Garreau and Rochambeau, 2003, Khalil *et al.*, 2005, 2007; El-Raffa 2007; Iraqi *et al.*, 2008; Sánchez *et al.*, 2008; Youssef *et al.*, 2008). In the last decade, a canalization procedure was also used in selection to reduce the sensitivity of selection for the environmental effects (Scheiner and Lyman, 1991; Hill, 2002). To provide an evidence for the control of environmental sensitivity, a statistical model has been proposed by San Cristobal *et al.* (1998) incorporating the classical genetic effects acting on the mean production level in addition to the other genetic effects acting on the residual variance. A multiple-trait model has a greater risk in yielding biased estimates of the genetic parameters (i.e., heritabilities, genetic correlations and selection responses) than a repeatability animal model, and, thus, all conclusions about the advantages of multiple-trait models should be evaluated with caution (Piles *et al.*, 2006).

Estimation of selection responses

Developing different reproductive techniques could facilitate the estimation of selection responses for productive traits in rabbits. Piles and Blasco (2003) suggested that response to selection for increased growth rate could be estimated in three ways: (1) comparing the selected group with the control group in a model without genetic effects, (2) comparing the selected group with the control group with a model that also included the genetic values of the animals, and (3) estimating the genetic values of all animals of the selection process then estimating the selection response as the average of the estimated genetic values in each generation. However, the most common methods used to estimate selection responses could be outlined as:

- 1) Using the control population that must be developed parallel to the selected population but without carrying out any selection (Rochambeau *et al.*, 1989, 1994, 1998; Sorensen and Johanson, 1992; Baselga, 2004; Sánchez *et al.*, 2004b) (i.e. the control population must be raised contemporaneously and under the same environment as the selected population). The control population has the advantage of providing information independent of the model used for the analysis of selected data. The main problems in using the control population in long-term experiments are: (a) the genetic drift acts on the control populations (usually for small size) and the estimate of the response to selection may be biased, and (b) the need for experimental facilities to be used in applying the selection program. Piles and Blasco (2003) stated that using frozen control populations have better advantages in optimizing the experimental facilities to reduce the genetic drift. Some bio-techniques, such as cryopreservation of embryos or semen, are used to avoid the disadvantages of maintaining the control population without selection. Cryopreserved control populations eliminate the effects of unintended selection on related traits that often occur and also decrease the effects of natural selection.
- 2) Comparing the contemporaries of two different generations by using frozen embryos of the same line (Santacreu *et al.*, 2000; García and Baselga, 2002a; Piles and Blasco, 2003; Gil *et al.*, 2006).

- 3) Using divergent selection to study the differences between two lines selected contemporarily in two directions, one direction to increase the trait and the second direction to decrease it, then contrasting both lines against the control population (Moura *et al.*, 1997; Santacreu *et al.*, 2000, 2005; Gondret *et al.*, 2002; Blasco *et al.*, 2005; Mocé *et al.*, 2005; Rafat *et al.*, 2007, 2008). In this concept, for example, Santacreu *et al.* (2005) estimated the correlated responses after 10 generations of divergent selection for litter size and its components (ovulation rate, and embryo survival and fetal survival) by contrasting both lines against a cryopreserved control population.
- 4) Using statistical methods such as mixed-model methodology and Bayesian approach that were used to estimate the genetic trends or selection responses and that are dependent on the model has been used (García and Baselga, 2002a, 2002b; Blasco *et al.*, 2005). Without the control population, Sorensen and Kennedy (1986) used mixed-model methodology to estimate the genetic response, but the results obtained by this method were highly dependent on the genetic parameters and the model used. Sorensen *et al.* (1994) provided a Bayesian way of estimating the selection response that has the advantage of taking into account the uncertainty about the variance components. Lukefahr *et al.* (1996) using mixed-model methodology estimated the responses of selection from regressing the breeding values (obtained from mixed-model analyses) or from regressing the differences between selected line and control line (from Richardson's method) on generation number. They reported that correlated responses in selected line for weaning weight and daily weight gain tended to be consistent between the two procedures. Both methods are model-dependent, and their reliabilities are dependent on the model proposed for the analysis. However, some selection experiments were analysed at the same time using two types of methods, and in most cases responses estimated by both types of approaches were in good agreement, but not always (Rochambeau *et al.*, 1998; García and Baselga, 2002a, 2002b, 2002c; Blasco *et al.*, 2003, 2005; Piles and Blasco, 2003; Tudela *et al.*, 2003; Mocé *et al.*, 2005; Santacreu *et al.*, 2005). Piles and Blasco (2003) estimated the direct selection responses in an experiment using the biotechnique of the frozen embryo transfer or using the statistical Bayesian approach; but both methods yielded similar estimates of responses.

Selection responses obtained from crossbred rabbits

In crossbreeding programmes followed by selection, it is necessary to evaluate the response of selection obtained in crossbred rabbits. Such an evaluation could be performed using one of the following approaches:

- 1) Evaluating crossbreeding parameters in the cross periodically with the aim of estimating these parameters (e.g., direct and maternal additive and heterosis, recombination effects) as performed in France, Spain, Egypt, Saudi Arabia, Brazil, etc.
- 2) Comparing heterosis estimates obtained from an experimental station with those of contemporary experiments on commercial farms as stated by Brun and Saleil (1994) who found that estimates of heterosis were remarkably similar for total litter size and number born alive, but lower on commercial farms than at experimental station for litter size at weaning.
- 3) Evaluating the genetic selection responses at different stages of the programme by conducting the contemporary comparisons among purebred and crossbreds as performed by Tudela *et al.* (2003) in France and Costa *et al.* (2004) in Spain. In these comparisons, the maternal lines involved in the French experiment were INRA1007 (rabbits of 30th generation of selection) and INRA9077 (control line), while in the Spanish experiment the maternal lines were A and V and line A with two different generations of selection. In the French experiment, both lines were crossed with another French line and the difference in total litter size between both types of crossbred does was 1.43 rabbit, a little higher than expected from selection in INRA1077 (1.12 rabbit). In the Spanish experiment, evaluation was performed on crossbred does from mating does of V line to bucks of line A, while crossbred rabbits were the progeny from crossing crossbred does with bucks of line R. Results of this Spanish experiment could be summarized as follows: (a) all selection responses

in litter size traits were in favour of crossbreds relative to purebreds since differences in total litter size, number born alive and number at weaning were 0.83, 1.16 and 0.74 rabbit, respectively (i.e., responses in crossbred does were higher than expected from the responses evaluated in the pure lines), (b) responses in crossbred progenies were lower than expected, since the response in post-weaning daily gain was 0.6 g/d, and (c) responses in feed conversion index improved.

APPLICATION OF MOLECULAR TECHNIQUES IN SELECTION

Major genes

Bosze *et al.* (2002) indicated that there was a major gene affecting litter size and that this gene gives a good evidence for a QTL mapping to be used in selection experiments. Argente *et al.* (2003a) and Santacreu *et al.* (2005) performed a complex segregation analysis for data of 10 generations of selection and they reported that there was a major gene with a large effect on implanted embryos and embryo survival and with a moderate effect on ovulation rate, foetal and prenatal survival and uterine capacity. However, this complex segregation analysis is imprecise, but these results agree with those observed by Blasco *et al.* (2005) in the first and second generation of selection. Hence, uterine capacity is highly genetically correlated with litter size as suggested by Argente *et al.* (2000), an asymmetric response in litter size should occur.

QTL analysis

Fadiel *et al.* (2003) analyzed 160 genes of rabbits depending on gene bank by providing useful information for designing more effective PCR primers in QTL analysis. Korstanje *et al.* (2003) mapped the individual rabbit chromosomes and found that the linkage group XI linked to chromosome 3 and the linkage group VI linked to chromosome 5. They also constructed four new linkage groups assigned to chromosomes 6, 7, 12 and 19. Chantry-Darmon *et al.* (2006) built up the first genetic map for Angora and Albino rabbits using 111 markers (109 microsatellites markers and two phenotypic markers). Van Haeringen *et al.* (2001, 2002) determined 226 polymorphisms between two inbred strains of rabbits by using 15 primer combinations of AFLP markers. They reported for the first time the first genetic male map in rabbits which has a distance of 583 cM. They found four QTLs with a LOD score (log of odds) larger than 1.9 and they identified also the QTL for the hematocrit value and for three parameters responsible for cholesterol metabolism [basal serum total cholesterol level (mM), serum total cholesterol response (AUC), and relative adrenal gland weight (mg/kg body weight)].

In divergent selection in rabbits for open-field activity (OFA), Sacharczuk *et al.* (2005) reported that selection has resulted in differences in DNA fingerprinting pattern and genetic parameters of diversity, and also scanned DNA fingerprinting profiles; leading to search for minisatellite alleles potentially linked to genes determining the trait under selection. Using rabbits derived from the 8th generation of the lines selected for high (H) or low (L) levels of OFA, locomotor OFA were profiled for DNA fingerprinting and the analysis of band patterns for individual and pooled DNA fingerprints revealed that a specific band in the L line at 15 kbp was detected, while in the H line specific bands were not detected; providing evidence of a possible linkage between minisatellites and OFA in rabbits, demonstrating that studies on H and L lines may give rise to a new strategy in animal breeding and selection.

Khalil *et al.* (2008) used RAPD markers to search for the linkage between markers and quantitative traits. They used 526 rabbits in this analysis from a sire-granddaughters design in their selection program. From a total of 40 primers (10-mer) used in their study, five primers (OPA12, OPA19, OPA20, OPF09, and OPF12) were able to identify five polymorphic fragments at molecular weights of 1500, 1100, 1200, 700 and 900 bp, respectively, and only three markers of these markers (OPF12₉₀₀, OPA19₁₁₀₀, and OPF09₇₀₀) showed significant associations with phenotypic traits, which indicated the presence of linkage between the three markers for litter weights at birth, 7 and 21 days,

and at weaning, litter gain at interval of 0-21 days, pre-weaning litter mortality, milk yield at lactation intervals of 0-7 and 0-21 days, and body weight at 4 and 8 weeks of age.

DIRECT AND INDIRECT SELECTION FOR DOE TRAITS

Selection criteria

The most common direct criteria used in selection programs of maternal lines were related with litter size at birth or at weaning (Estany *et al.*, 1989; Gómez *et al.*, 1996, 2002b; Rochambeau *et al.*, 1998; Capra *et al.*, 2000; El-Raffa, 2000; Baselga and García, 2002; García and Baselga, 2002a, 2002b). In some cases, selection criteria included litter size at birth and weight at nine weeks (Bolet and Saleil, 2002), number of teats (Rochambeau *et al.*, 1988), while in other cases selection programs were practiced for traits related with the ability of the doe for lactating and nourishing the progeny, such as weight at weaning (Garreau and Rochambeau, 2003), litter weight at weaning or total milk production (Khalil *et al.*, 2002; Al-Saef *et al.*, 2008; Iraqi *et al.*, 2008; Youssef *et al.*, 2008). Fortun-Lamothe (2003) and Quevedo *et al.* (2006b) demonstrated that lactation is a priority trait for selection of the crossbred doe by taking into account competition between foetal growth and lactation, which is unfavourable for foetal growth. Selection for ovulation rate and uterine capacity has been successfully performed as indirect ways for improving prenatal survival and litter size in rabbits (Bennett and Leymaster, 1989; Ibañez *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, 2006, 2007) and reducing this heterogeneity might be useful in selection program 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.*, 1998a; Santacreu *et al.*, 2000). Longevity has been introduced recently in rabbit selection programs (Sánchez *et al.*, 2004a, 2008) although it is difficult to improve this trait through conventional breeding methods because of the low heritability and the time needed to obtain information. Sánchez *et al.* (2004a) concluded that both longevity and litter size are not antagonistic objectives in breeding programs because selection for one does not influence the other.

Techniques assisted in selection programs

New techniques (laparoscopy, ovariectomization, cryopreservation of embryos and semen, etc.) were used commonly as tools assisted in selection programs in rabbits. Blasco *et al.* (1994) and Bolet *et al.* (1994) reported that litter size in unilaterally ovariectomized does could be used to estimate uterine capacity in rabbits. Also, it is possible to observe the number of corpora lutea and implantation sites by laparoscopy without impairing litter size as verified by Santacreu *et al.* (1994, 1996).

Selection methods and procedures used

Rabbit litter size is mainly determined by the doe component, whereas the buck has a very small effect; therefore, it seems unnecessary to include the buck component in selection models (Piles *et al.*, 2006). In Spain, Estany *et al.* (1989) applied a family index including four sources of information (doe, dam of doe, full sisters and paternal or maternal half-sisters) to evaluate does or bucks for litter size at weaning of line A. Gómez *et al.* (1996) and Rochambeau *et al.* (1998) used a BLUP procedure in evaluation of does and bucks since this procedure is quite different from a family index in that some environmental and physiological effects are considered in the model. Response to selection would probably be the same if selecting for litter size under a repeatability animal model or using a selection index and this is because the accuracies of predicted breeding values obtained under the two models are nearly equal (Piles *et al.*, 2006).

A selection experiment for ovulation rate was practiced in the second gestation by laparoscopy in Spain where the animals were derived firstly from a synthetic line selected for litter size for 12

generations, then for uterine capacity for 11 generations, and then 5 generations in which selection was relaxed (Ibañez *et al.*, 2004). A divergent selection experiment was carried out by Garreau *et al.* (2004b) at the INRA experimental farm and a new model incorporating the genotypic value for the mean and the genotypic value for the residual variance (canalization procedure) was applied to select for homogeneity of birth weight in the litter and to estimate the correlated responses in other traits and to provide new issues relevant to validate this innovative statistical method.

Selection effect and direct responses

As presented in Table 1, genetic responses obtained from long-term selection experiments for litter size and other litter traits were found to be moderate. Some responses in litter traits were estimated exclusively by mixed-model methods (Estany *et al.*, 1989; Rochambeau *et al.*, 1994; Gómez *et al.*, 1996) where the estimates ranged from 0.05 to 0.129 rabbits born alive or weaned per litter and generation.

Table 1: Direct and correlated selection response per generation obtained for doe traits in selection experiments selected for litter size or ovulation rate or uterine capacity.

Authors	Breed or line	Methodology	Direct and/or correlated selection responses [†]
Selection for litter size:			
Gómez <i>et al.</i> (1996)	Line PRAT	Genetic trend using BLUP methodology	LSW = 0.09 rabbit per year
Rochambeau <i>et al.</i> (1998)	INRA1077	Genetic trend using a control population and applying BLUP methodology	LSW = 0.081 rabbit per generation
García <i>et al.</i> (2000a), (2000b)	Line V	Comparing contemporaries using cryopreservation (vitrification) population	LSW = 0.088 rabbit per generation No correlated responses were obtained for growth, feed consumption and feed efficiency traits
García and Baselga (2002a), (2002b)	Line V	<ul style="list-style-type: none"> Genetic trend using cryopreservation control population and mixed-model methodology Contemporaries using cryopreservation control population and mixed-model methodology Genetic trend using mixed-model methodology 	Direct responses of LSW= 0.51 rabbit per litter or 0.085 rabbits per generation; with correlated responses of LSB= 0.62 rabbit per litter or 0.103 rabbit per generation; NBA= 0.57 per litter; OR = 1.08 per litter or 0.18 ova per generation; IE= 0.74 per litter; DF= 0.05 per litter; IR = - 0.14 per litter; FS = 2.18 per litter; PS = 0.34 per litter Direct responses of 0.77 weaned rabbit per litter; with correlated responses of OR = 0.03 ova per litter; IE = - 0.15 per litter; DF = - 0.63 per litter; IR= -1.44 % per litter; FS = 5.7 % per litter; PS= 3.7 % per litter; LSB = 0.78 rabbit per litter; NBA = 0.74 rabbit per litter; Number at 63 d = 0.5 rabbit per litter LSB = 0.161 rabbit per generation; NBA = 0.175 rabbit per generation; LSW = 0.175 rabbit per generation; No at slaughter = 0.191 rabbit per generation
Selection for uterine capacity:			
Blasco <i>et al.</i> (2005)	Synthetic population	Genetic trend in divergent selection using Bayesian method	Divergence rate = 1.5 rabbits per generation
Mocé <i>et al.</i> (2005)	derived from crossing NZW and Californian	Genetic trend in divergent selection using Bayesian method	Per litter: LSB = - 0.008 rabbits; NBA = 0.20 rabbits; OR = - 0.009 ova; IE = - 0.60; ES = - 0.05; FS = 0.08; PS = 0.02
Santacreu <i>et al.</i> (2005)	Californian	Genetic trend in divergent selection using Bayesian method	Per litter: LSB = 0.47 rabbits; NBA = 0.15 rabbits; OR = - 0.32 ova; IE = - 0.28; ES = 0.04; FS = 0.04; PS = 0.05
Selection for ovulation rate:			
Ibañez <i>et al.</i> (2006)	Line V	Genetic trend in phenotypic selection using Bayesian method in analysis	Per litter: OR = 1.8 ova; IE = 1.44; LS = 0.49 rabbits; Prenatal survival = - 0.009; ES = 0.05; FS = - 0.09

[†]LSB: litter size at birth; NBA: number born alive; LSW: litter size at weaning; OR: ovulation rate; IE: implanted embryos; DF: number of dead foetus; ES: embryo survival; IR: implantation rate; FS: foetus survival; PS: prenatal survival.

In other cases, Rochambeau *et al.* (1998), García and Baselga (2002a, 2002b), and Tudela *et al.* (2003) reported that direct responses ranged from 0.08 to 0.14 rabbits for total number born, number born alive or weaned per litter and generation; responses estimated as genetic trends or by mixed-model were nearly similar. These responses were lower than expected and this could be attributed to: (1) additive genetic variance for litter size at weaning was low, (2) heterogeneity between parities was high (Baselga *et al.*, 1992), (3) correlations between direct and maternal effects were negative, and (4) intensity of selection was low.

Mocé *et al.* (2004, 2005) and Blasco *et al.* (2005) found that direct response to selection for uterine capacity was symmetric and they stated that selection for uterine capacity in rabbits leads to modifications in embryonic and fetal survival. The divergence rate between high and low lines in such selection experiments were 1.01 rabbits for litter size at birth, 0.88 rabbits for number born alive, 0.16 ova for ovulation rate, 0.46 embryo for implanted embryos, 0.03 embryo for embryo survival, 0.09 fetus for fetal survival, and 0.08 for prenatal survival. Garreau *et al.* (2004b) reported that selection for homogeneity of birth weight in the litter had no significant influence on other litter traits.

Selection effect and correlated responses

Rochambeau *et al.* (1988) found that number of teats increased indirectly in a population selected for litter size at weaning respective to the control population. As shown in Table 1, selection for ovulation rate was associated with a correlated increase in litter size compared to direct selection for litter size as reported by Santacreu *et al.* (2005) in Spain, while selection for uterine capacity was associated with indirect response in number of teats as reported by Mocé *et al.* (2000) in France.

Selection for litter size in rabbits showed that the magnitudes of correlated responses in the components of litter size were varied from one experiment to another (Quevedo *et al.*, 2006a, 2006b). García and Baselga (2002a, 2002b) showed that selection for litter size was associated with an increase in ovulation rate (0.18 more ova for ovulation rate per generation) with non-significant changes for prenatal survival. However, differences for embryo survival may be due to differences in fertilization rate, embryo viability, or other factors related to the oviduct or/and uterine physiology of the doe. Ibañez *et al.* (2004) reported that selection response for ovulation rate was 0.97 ova, while the correlated responses for implanted embryos and litter size were found to be 0.79 embryo and 0.32 rabbit, respectively. After 10 generations of divergent selection, the correlated responses obtained by Santacreu *et al.* (2005) for litter size and its components (ovulation rate, embryo survival, and fetal survival) were asymmetric, divergence rate between high and low lines was 2.35 rabbits, mainly because of higher correlated response in the low line (1.88 rabbits).

Selection for uterine capacity for several generations has been performed successfully in rabbits, and it produced a response that was similar to that found in experiments in which direct selection for litter size was practiced (Argente *et al.*, 1997; Blasco *et al.*, 2000, 2005; Santacreu *et al.*, 2005) (Table 1). The observed increase in litter size caused by selection for uterine capacity was not greater than the improvement obtained from direct selection for litter size (approximately 0.1 rabbits per litter per generation), while the correlated response in number born alive was asymmetric and less than that for litter size (Rochambeau *et al.*, 1998; García and Baselga, 2002a, 2002b). Argente *et al.* (2000) found a large genetic correlation between litter size and uterine capacity, which supports the non-asymmetric response in uterine capacity as detected by Blasco *et al.* (2005). The correlated selection divergence rate for uterine capacity between high and low lines reported by Santacreu *et al.* (2005) were 2.35 rabbits in litter size at birth (reflecting the role of a major gene affecting uterine capacity and litter size as stated as Bosze *et al.*, 2002 and Argente *et al.*, 2003a), associated with 1.84 rabbits for number born alive, 0.43 ova for ovulation rate, 1.79 embryo for implanted embryos, 0.10 embryo for embryo survival, 0.13 fetus for fetal survival, and 0.19 for prenatal survival, while the respective selection difference between high and control line were 0.47, 0.15, -0.32, -0.28, 0.0, 0.04, and 0.05.

Quevedo *et al.* (2005, 2006b) found that does selected for litter size at weaning presented significantly higher feed intake (3%) and milk yield (6%) during the first 21 days of lactation, while the responses

at late stages of lactation were not significant. Selection effects on weaning weight (28 days) reported recently by Quevedo *et al.* (2006) agrees with the results obtained by García and Baselga (2002c), who found that the effects of selection for litter size at weaning on weaning weight corrected for litter size at birth were limited. For data not corrected for litter size, the individual weaning weight was decreased by selection (Costa *et al.*, 2004). In contrast, Khalil *et al.* (2004) reported that selection responses for litter weight at weaning was 62 g per litter; associated with a correlated response of about 0.17 rabbit per litter per generation for litter size born and weaned.

Selection programs in synthetic maternal lines developed

Summaries for maternal lines developed through selection are presented in Table 2.

Table 2: Selection programs in synthetic maternal lines developed in some parts of the world

Synthetic line and authors	Founder breeds	Selection criteria	Selection methodology	Number (interval) of generations	Selection response per generation+
French selection experiments:					
INRA2066, Bolet and Saleil (2002)	Californian, Giant Himalayan	Birth litter size	BLUP procedure	More than 34 generation	LSB= 0.12 rabbit per litter; LSW= 0.07 rabbit per litter; LWW= 34 g per litter; WW= -4.4 g per rabbit
INRA2666, Bolet and Saleil (2002)	INRA2066 and V-Line	Litter size	BLUP procedure		
INRA1777, Garreau and Rochambeau (2003)	INRA1077	Birth litter size + weaning weight + longevity	BLUP procedure	More than five generations	
Spanish selection experiments:					
Line A, Estany <i>et al.</i> (1989)	NZW	Weaning litter size	Family index including litter size at weaning of doe, dam, full-sisters and half-sisters	More than 33 generation (9 months)	LSW= 0.1 rabbit
Line V, Estany <i>et al.</i> (1989)	Four specialized maternal lines	Weaning litter size	BLUP procedure under an animal-repeatability model	More than 30 generation (9 months)	LSW= 0.03 rabbit
Line PRAT, Gómez <i>et al.</i> (1996), (2002b)	A closed population with crossbred animals	Weaning litter size	BLUP procedure under an animal-repeatability model		
Line H, García-Ximenez <i>et al.</i> (1996)	Hyper-prolific V line does	Birth litter size	BLUP with applying embryo cryo-preservation technique	More than 11 generation (9 months)	
Line LP, Sánchez <i>et al.</i> (2008)	Line H	Hyper-longevity + Birth litter size	BLUP procedure		
Selection experiments in developing countries:					
Saudi-2, Saudi Arabia, Khalil <i>et al.</i> (2005)	V line and Saudi Gabali	Weaning litter weight + 84-d weight	BLUP procedure under an animal-repeatability model	More than 10 generations (9 months)	LSB= 0.18 rabbit per litter; LSW= 0.16 rabbit per litter; LWW= 62 g per litter; WW= 8.6 g per rabbit
APRI, Egypt, Youssef <i>et al.</i> (2008)	V line, Baladi Red	Weaning litter weight	BLUP procedure under an animal-repeatability model	More than 5 generations	
Uruguay NZW, Capra <i>et al.</i> (2000)	NZW	Weaning litter size	BLUP procedure	More than 5 generations	
Uruguay V, Capra <i>et al.</i> (2000)	V line	Weaning litter size	BLUP procedure	More than 5 generations	

+LSB: litter size at birth; NBA: Number born alive; LSW: litter size at weaning; LWW: litter weight at weaning; WW: weaning weight.

In France, a maternal line of INRA2066 was directly selected for litter size at birth and this line was used to produce the most common parental female of INRA1077 x INRA2066 (Rochambeau, 1998; Bolet and Saleil, 2002; Garreau *et al.*, 2004a). A new selection experiment was started in 2003 to develop the line INRA1777 through selection for litter size at birth, together with individual weaning weight (Garreau and Rochambeau, 2003); longevity was added later as a new criterion (Garreau *et al.*, 2001, 2004a).

In Spain, long-term selection experiments were carried out to produce synthetic lines to be used on commercial farms. Details concerning these new lines were presented by Baselga (2004). In 1976, the Spanish line A was developed from NZW rabbits and selection was practiced using a family index including litter size at weaning of the doe, dam, full-sisters and half-sisters. The Spanish line V was founded in 1981 as a synthetic line and this line was selected for litter size at weaning using a BLUP procedure under an animal-repeatability model (Estany *et al.*, 1989). In 1992, the PRAT line was developed in Barcelona from a closed population (with 178 crossbred animals). In this line, selection was practiced for litter size at weaning using a BLUP procedure under an animal-repeatability model (Gómez *et al.*, 1996). The foundation of line H was based on the detection of hyperprolific does and this line is selected for litter size at birth. Recently, a new maternal line in Spain named LP was established following a scheme similar to that applied in selection for hyperprolificacy taking hyperlongevity and litter size as selection criteria. Details concerning constitution and evaluation of such a long-lived productive line of rabbits were presented by Sánchez *et al.* (2008).

In Saudi Arabia, Saudi 2 was synthesized from crossing Saudi Gabali with V-line rabbits (75% from V line and 25% from Saudi Gabali) and selected for litter weight at weaning and individual weight at 84 d. Details concerning the development of this new line were presented by Khalil *et al.* (2002, 2005) and Al-Saef *et al.* (2008).

In Egypt, Baladi Red bucks (B) were mated with V line does to produce a new synthetic line named APRI with genetic structure of $((\frac{1}{2}B\frac{1}{2}V)^2)^2$. This line was selected for litter weight at weaning. In Uruguay, two lines were developed through selection for litter size at weaning, where the first line named Uruguay NZW and the second line named Uruguay V-line (Capra *et al.*, 2000).

DIRECT AND INDIRECT SELECTION FOR GROWTH, CARCASS AND MEAT QUALITY TRAITS

Selection criteria

Selection for rapid growth rate has been largely introduced to develop sire lines to modify the whole pattern of growth, feed efficiency, and tissue composition, thus affecting carcass and meat quality traits. Current programs of rabbit selection normally include terminal sires produced from selection schemes commonly practiced for post-weaning daily gain (Rochambeau *et al.*, 1989; Estany *et al.*, 1992; Hernández *et al.*, 1997, 2004; Moura *et al.*, 1997; Piles *et al.*, 2000, 2004; Gómez *et al.*, 2002a; Sánchez *et al.*, 2004b; El-Raffa, 2007) or for body weight at the market age (Lukefahr *et al.*, 1996; Gondret *et al.*, 2002; Khalil *et al.*, 2002, 2005; Larzul *et al.*, 2005; Al-Saef *et al.*, 2008). In practice, criterion of post-weaning growth is effective in selection programs because it is very easy to record and it has a negative and favourable genetic correlation with feed conversion index, and therefore this trait is very important for an efficient rabbit production (Moura *et al.*, 1997; Piles *et al.*, 2004).

The average daily gain is the preferred trait for selection during post-weaning period, suggesting that individual selection could be used successfully to improve this trait because this trait is less affected by common litter effects than the individual weights at specific ages and it has moderate or high heritabilities that vary in magnitude from 0.13 to 0.48 (Rochambeau *et al.*, 1989; Estany *et al.*, 1992; Ferraz and Eler, 1996; Krogmeier *et al.*, 1994; Lukefahr *et al.*, 1996; McNitt and Lukefahr, 1996; Moura *et al.*, 1997; García and Baselga, 2002c; Piles *et al.*, 2004). Moura *et al.* (1997) stated that selection based on an index including both growth rate and feed conversion ratio would be more

efficient for improving feed efficiency than selecting solely for growth rate. Although feed conversion ratio is the most important trait in meat rabbit production (Armero and Blasco, 1992; Piles *et al.*, 2004), this criterion was not considered commonly in selection programs. Baselga (2004) reported that feed conversion index is not used directly in selection because it is expensive to record and would need electronic devices to enable recording of individual feed intake. Since feeding costs represent about 70% of the rabbit meat production costs, feed conversion (g feed per g gain) could be an economic trait in direct selection (Moura *et al.*, 1997; Larzul and Rochambeau, 2005).

Techniques assisted in selection programs

Applying the technique of TOBEC (Total Body Electrical Conductivity), Milisits and Levai (2002) demonstrated that selection for TOBEC value was associated with indirect improvement in carcass composition, observing a difference of 22.6% between animals selected for low and high fat content. A technique of X-ray computerized tomography (CT) was utilized to assess *in vivo* body composition in selection of rabbits (Nagy *et al.*, 2006) and this technique of selection was used successfully in sheep in UK, Australia and New Zealand (Simm, 1987; Jones *et al.*, 2002, 2004). Using such technique in rabbit research are summarised by Romvári *et al.* (1996) and the results of using CT as an aid of selection in Pannon White rabbits were reported by Szendrő *et al.* (1996) and Nagy *et al.* (2006) taking into account the genetic correlations between average cross-sectional area of *m. Longissimus dorsi* (measured by CT) and a carcass trait (Szendrő *et al.*, 1992). However, high scanning costs in evaluating the animals by CT would be a limiting factor to use such technique in selection program.

Szendrő *et al.* (1996, 2004) selected indirectly for daily gain and carcass quality in Pannon White breed by measuring the average surface of *m. Longissimus dorsi* (L value) at 10.5 weeks of age by using a computerized tomography technique and applying BLUP for L-value to select growing rabbits. A two-step procedure of selection was used where the first step was for daily weight gain between 5 and 10 weeks of age, and the next one was for the L-value obtained from CT scanning. Results demonstrated that rabbits with higher L-values in *m. Longissimus dorsi* were associated with higher meat weight of the hind legs (Szendrő *et al.*, 1992). The effectiveness of selection for carcass traits was confirmed by Metzger *et al.* (2004) and Szendrő *et al.* (2004) using CT technique to compare between different genotypes (Pannon White, Hyplus, and their crosses). In this experiment, BLUP for L-values measured for the scanned animals showed that selection based on CT measurement could be effective to improve carcass traits in rabbits.

Selection methods

In general, individual mass selection was used as the common methodology to select for growth traits in paternal lines of rabbits and this is because this method is the simplest procedure to be applied for heritable traits expressed in both sexes. By this way, time, labour and resources can be reduced and the generation interval could be shortened to about 6 mo (Baselga, 2004). Since average daily gain in weight and feed conversion are moderately to highly heritable, having high and negative genetic correlations between them, applying mass selection for average daily gain was associated with favorable correlated selection responses (Feki *et al.*, 1996; Moura *et al.*, 1997). Lukefahr *et al.* (1996) concluded that individual selection was effective for increasing marketing weight following five generations of selection.

A two-way selection experiment for improving average daily gain and feed conversion was performed by Moura *et al.* (1997) who reported that this program could be performed at least in the first generations of selection without difficulties in measuring feed consumption. Another divergent selection experiment was performed by Larzul and Rochambeau (2005) in order to estimate the consequences of selection for feed efficiency (30-65 d) on growth, feed efficiency, and carcass composition (fatness of the males was estimated using the technique of TOBEC at 65 days of age). Piles *et al.* (2004) concluded that growth rate and feed conversion ratio should be used in an index in order to improve the selection response for feed conversion ratio, which is the most important trait in

rabbit production (i.e., feed conversion ratio would be improved by more than 77% if an index including growth rate and feed conversion ratio was used compared to indirect selection using growth rate).

Progeny testing was practiced to select directly for dressing out percentage (Nagy *et al.*, 2006), although the costs of this method are high and it lengthens the generation interval. This method was practiced previously by Varewyck *et al.* (1986) and Szendrő *et al.* (1988).

Selection effect and direct responses

Selection experiments for growth rate in rabbits reporting successful responses in most experiments (Table 3). In this concept, direct selection responses for average daily gain or for body weight at market time were verified (Mgheni and Christensen, 1985; Lukefahr *et al.*, 1996; McNitt and Lukefahr, 1996; Moura *et al.*, 1997; Blasco *et al.*, 2003; Piles and Blasco, 2003; Nagy *et al.*, 2006), while in some cases the responses were less than expected (Rochambeau *et al.*, 1989; Estany *et al.*, 1992; Gondret *et al.*, 2002; Sánchez *et al.*, 2004b). Such contradictions in results of selection responses may be due to the overlapping of generations, especially when a control population was not used in the same generation of the selected population, or may be due to the appearance of a disease such as enterocolitis.

Table 3: Direct and/or correlated selection response per generation obtained for growth and carcass traits in selection experiments

Authors	Breed or line	Selection criteria	Methodology	Direct and/ or correlated selection responses ⁺
Rochambeau <i>et al.</i> (1989)	INRA1077	Growth rate (4-11 wks)	Genetic trend for phenotypic selection using mixed-model	ADG= 0.83 g/d per year
Lukefahr <i>et al.</i> (1996)	F ₂ population of ½ Flemish Giant, ¼ Californian, ¼ Champagne	70-day weight (market weight)	Genetic trend for phenotypic selection using mixed-model	Per generation: W70= 29.4 g; WW = 9.5 g; ADG (28-70 d) = 0.47 g/d; CY = - 0.24%; PL = -0.04%; MBR = 0.1
Garreau <i>et al.</i> (2000)	White Pannon	Growth rate (6-10 wks)	Annual genetic trends using BLUP in multiple-trait model.	ADG = 0.64 g/d per year; W10 = 18.5 g per year.
García and Baselga (2002c)	Line V	Litter size at weaning	Contemporaries using control cryopreserved population and mixed-model methodology	Per generation: WW = 1.4 g/d; ADG (28-63 d) = 0.11 g/d; W63 = 1.5 g/d; FC = -3.3 g/d feed; FCI = 0.01; For all traits, the responses were less than 0.3% of the population mean.
Piles and Blasco (2003)	Synthetic line selected for growth rate	Growth rate (4-9 wks)	Phenotype selection using control population and Bayesian inferences	Growth rate = 7% relative to the population mean before selection
Hernández <i>et al.</i> (2004)	Line R	Growth rate (9-13 wks)	Contemporaries using control population (differences between selected and control groups)	Per generation: SW = 118 g; CCW = 53 g; DP = - 0.22%; PL = 0.23%; KP = 0.04%; LHP = 0.02%; RCW = 46 g; FP = -0.3%; LP = 0.6%; MBR = 0.42
Sánchez <i>et al.</i> (2004b)	Line R	Daily gain (28-63 d)	Contemporaries using cryopreserved population (as control) and an animal model	Per generation: ADG= 0.18 g/d; WW= 8.7 g; W63= 94.6 g; FC= 0.05 g feed per g gain

⁺WW: weaning weight; W10: weight at 10 weeks; W63: weight at 63 d; SW: slaughter weight; W70: marketing weight at 70-d; ADG: average daily gain; CY: carcass yield percentages (hot carcass weight/preslaughter weight times 100); PL: percent of liver; LP: loin percent; MBR: meat to bone ratio; FC: feed consumption; FCI: feed conversion index; CCW: chilled carcass weight; DP: dressing percent; KP: kidney percent; LHP: set of organs percent (thymus + trachea + esophagus + lungs +heart); RCW: reference carcass weight; FP: dissectible fat percent.

The rate of genetic progress in marketing weight per generation (29.4 g or 1.3% per generation) obtained by Lukefahr *et al.* (1996) was similar to the annual genetic improvement often reported for this trait in other livestock species (i.e., producers willing to select for increased 70-day body weight

may have genetic improvement in weaning weights and in average daily gains and also in lean-to-bone ratio). Using a control line or mixed-model methodology, direct responses obtained for growth rate from weaning to marketing age were moderate and ranged from 0.45 to 1.73 grams per day per generation for daily weight gain, while the responses for weight at market age ranged between 18 and 68 g per generation (Rochambeau *et al.*, 1989, 1994; Estany *et al.*, 1992; Lukefahr *et al.*, 1996; Moura *et al.*, 1997; Szendrő *et al.*, 1998; Garreau *et al.*, 2000; Khalil *et al.*, 2002, 2005; Hernández *et al.*, 2004; Sánchez *et al.*, 2004b). At commercial slaughter age (9 wk), Blasco *et al.* (2003) and Piles and Blasco (2003) found that selected animals had a higher growth rate of 7% relative to the population mean before selection and the slaughter weight was also higher in the selected group. However, weaning weight remained practically the same where the two methods used in estimating the selection response (control population vs. Bayesian inference) yielded similar results, thus validating the model used for the analysis. Gondret *et al.* (2002) and Larzul *et al.* (2005) found that body weights have been increased by selection, while carcass and muscle traits did not differ significantly between highly selected animals and the animals of a cryopreserved control population.

Selection effect and correlated responses

The estimates of correlated selection responses for growth, feed conversion and carcass traits available in literature are limited and the only available estimates are presented in Table 3. However, selecting at a fixed slaughter weight was associated with increases in feed consumption and decreases in feed conversion (Feki *et al.*, 1996); intestinal content increased, and dressing percentage decreased (Gómez *et al.*, 1998; Pla *et al.*, 1998), fat deposits reduced, ultimately pH in muscle and water holding capacity of the meat diminished (Piles *et al.*, 2000; Gondret *et al.*, 2003).

With regards to correlated selection responses for feed efficiency, resulting from direct selection for growth rate, some investigators (Torres *et al.*, 1992; Feki *et al.*, 1996; Moura *et al.*, 1997; Larzul and Rochambeau, 2005) found that selection for growth rate was associated with an improvement in feed efficiency. Heritability values for growth rate and feed conversion ratio were moderate or high and the correlations between both traits were also moderate or high (-0.82 as cited by Moura *et al.*, 1997; from -0.4 to -0.49 as cited by Piles *et al.*, 2004). In two elliptical selection experiments, Piles *et al.* (2004) indicated that selection for growth rate was expected to yield a similar correlated response for feed conversion ratio in sire Caldes and R lines of rabbits. In contrast, the effects of selection for growth rate on post-weaning feed intake were not significant (Costa *et al.*, 2004; Piles *et al.*, 2004; Sánchez *et al.*, 2004b).

Few experiments have assessed the consequences of selection for growth rate on carcass and meat quality traits in rabbits. In this respect, Lukefahr *et al.* (1996) reported that selection for marketing weight was associated with favorable correlated responses in daily weight gain and lean to bone ratio. However, the correlated responses were not significantly different from zero for growth traits, but the correlated responses for carcass traits were all positive and significant (Table 3). Comparing Richardson's procedure with mixed-model procedure, similar correlated responses of 0.1 and 0.21 units per generation of selection were observed in the selected line for lean to bone ratio. Hernández *et al.* (2004) indicated that selection for growth rate has little effect on carcass characteristics when rabbits were measured at the same stage of maturity because there was no increase in fat content of the carcass and there was an improvement in the meat-to-bone ratio, while meat quality at the same stage of maturity was affected a little by selection, only producing a decrease in water holding capacity (Table 3).

Piles *et al.* (2000, 2006), Gondret *et al.* (2002), Ramirez *et al.* (2004) and Gil *et al.* (2006) reported that genetic selection for growth rate did not affect carcass traits, muscle traits, protein degradation of *longissimus* muscle, and meat texture properties. In contrast, Piles *et al.* (2004) reported that selection for growth rate was associated with decreases in feed conversion rate, but may have also been associated with decreases in carcass and meat quality. By comparing two lines selected for live body weight at 63 days of age, and using a cryopreserved control population raised contemporaneously with selected rabbits of 5th generation, Larzul *et al.* (2005) attained considerable correlated selection

responses in growth rate, carcass, and muscle traits. Rochambeau *et al.* (1994) and Quevedo *et al.* (2005) reported that selection for increased litter size resulted in a decrease in individual weight at weaning, although total weight of the litter at weaning increased. Modifications in the selection objective for maternal lines were attempted by Rochambeau (1998) by including the weight at 63 days in addition to litter size to increase simultaneously litter size and individual weight.

As presented in Table 3, when the comparisons were done at a constant litter size at birth, the correlated responses in growth traits obtained from selection for litter size at weaning did not show any significant responses for weaning weight, weight at market time, post-weaning daily gain, daily feed intake and feed conversion index (Baselga and García, 2002; García and Baselga, 2002c).

Selection programs in synthetic paternal lines developed

The paternal lines developed for use on small and large commercial scales are presented in Table 4.

Table 4: Selection programs for synthetic paternal line development

Synthetic line and country of work	Authors	Founder breeds	Selection criteria	Selection methodology	Number (interval) of generations	Selection responses per generation ⁺
Line R, Spain	Estany <i>et al.</i> (1992)	Californian, specialized paternal line	Growth rate (28-63 d)	Individual selection using BLUP	12 generation, (6 mo)	ADG= 0.5 g/d
Altex, USA	Lukefahr <i>et al.</i> (1996)	Californian, Champagne d' Argent, Flemish Giant	70-day market weight	Individual selection using mixed-model	More than eight generations	W70= 29.4 g; WW = 9.5 g; ADG (28-70 d) = 0.47 g
White Pannon, Hungary	Szendrő <i>et al.</i> (1998)	NZW, Californian	Growth rate (6-10 wks)	Individual selection using BLUP	Since 1992	ADG= 0.6 g/d per year
Alexandria, Egypt	El-Raffa (2007)	Line V, Baladi Black	Daily body weight gain (28-63d)	Individual selection using BLUP	More than five generations, (10 mo)	
Saudi-3, Saudi Arabia	Khalil <i>et al.</i> (2002), (2005)	Line V and Saudi Gabali	Weaning litter weight + 84-d weight	Individual selection using BLUP	More than eight generations (9 mo)	W12= 38 g; ADG= 0.6 g/d; LSB= 0.14 rabbits per litter; LSW= 0.12 rabbits per litter; LWW= 35 g per litter

⁺ADG: average daily gain; WW: weaning weight; W70: weight at 10 weeks; W12: weight at 12 weeks; LSB: litter size at birth; LSW: litter size at weaning; LWW: litter weight at weaning.

In Hungary, White Pannon rabbits were created since 1991 by crossing New Zealand White rabbits with Californian and then selection was practiced for growth rate between 6-10 weeks of age (Szendrő *et al.*, 1998). In Spain, line R was individually selected for daily gain between 28-63 days and the main objective of selection was directed to improve feed efficiency; this line was developed for use on commercial farms (Estany *et al.*, 1992). In USA, Lukefahr *et al.* (1996) described the development of a large terminal-sire breed, known as the ALTEX, selected for 70-day market weight, which has a breed foundation of ¼ Californian, ¼ Champagne d' Argent, and ½ Flemish Giant. In Saudi Arabia, Saudi-3 was established from ¼ V line and ¾ Saudi Gabali and selected for litter weight at weaning and individual weight at 84 d. The details concerning the development of this new line were presented by Khalil *et al.* (2002, 2005) and Al-Saef *et al.* (2008). In Egypt, a synthetic paternal line of Alexandria originated at Alexandria University from crossing V line with the Baladi Black, and selection was practiced for daily weight gain during 28-63 days of age (El-Raffa, 2007).

DIRECT AND INDIRECT SELECTION FOR TOTAL OBJECTIVES

Criteria and methods of selection

Ramon *et al.* (1992) and Utrillas *et al.* (1992) proposed demographic and phenotypic analyses in a synthetic population of rabbits selected for total objectives of litter weight at 60 days through overlapping generations. However, multi-purpose lines were developed as a total objective through simultaneous selection for litter size and growth traits. This selection strategy was successfully developed in Spain, France, Brazil, and Egypt. In Spain, a two-stage selection program was practiced using two criteria (litter size at weaning and individual daily weight gain) and applying the method of independent culling level of selection (Gómez *et al.*, 2000a), while the French program of selection was practiced for litter size at birth and individual weight at 63 days (Rochambeau, 1998; Garreau and Rochambeau, 2003). In Brazil, a selection index including litter size at weaning, individual weaning weight, weaning litter weight and individual weight at 70 days of age was used (Moura *et al.*, 2001), while in Egypt, selection was practiced for litter weight at weaning and individual weight at 56 days (Youssef *et al.*, 2008).

Multi-purpose synthetic lines developed

Table 5 shows multi-purpose synthetic lines developed in some parts of the world.

Table 5: Selection programs for the development of multi-purpose synthetic lines

Synthetic line and country of work	Authors	Founder breeds	Selection criteria	Selection methodology	Direct response per generation ⁺
INRA1077, France	Bolet and Saleil (2002)	NZW, Bouscat	Weaning litter size then birth litter size + 63 d weight	Individual selection applying BLUP	LSB= 0.11 rabbits per litter; LSW= 0.08 rabbits per litter; LWW= 47 g; WW= - 3.4 g
Botucatu, Brazil	Moura <i>et al.</i> (2001)	Norfolk English line	Weaning litter size and weight + growth rate (28-70 d)	Selection index	
Caldes, Spain	Gómez <i>et al.</i> (2002a)	Six lines in Caldes de Montbui, Barcelona	Litter weight at 56-d weight + growth rate (32-60 d)	Two-stage selection applying BLUP	LWW= 30.7 g; ADG= 1.1 g/d
Giant de España, Spain	López and Sierra (2002)	Flemish Giant, Lebrél Español	Weaning litter size + growth rate during fattening	Independent culling levels selection	
Moshtohor, Egypt	Iraqi <i>et al.</i> (2008)	Sinai Gabali, line V	Litter weight+ 56-d weight	Two-stage selection using BLUP	

⁺LSB: litter size at birth; LSW: litter size at weaning; LWW: litter weight at weaning; WW: weaning weight; ADG: average daily gain.

In France, a multi-purpose line of INRA1077 was developed by selecting for litter size at birth and for individual weight at 63 days to produce the most common parental females of INRA1077x INRA2066 (Bolet and Saleil, 2002; Garreau and Rochambeau, 2003). From 1983 to 1992, the Caldes line in Spain was formed by selecting for litter weight at weaning in the first stage, while in the second stage the individuals were chosen for post-weaning growth. Since 1992, animals of this line are selected for growth rate between 32 and 60 days. Details concerning the foundation breeds and selection methods used in developing the Caldes line were described by Rafel *et al.* (1988) and Utrillas *et al.* (1992). In Brazil, a multi-purpose selection program was initiated in 1992 to develop a multi-purpose line using a selection index, including litter size and weight at weaning and post-weaning growth traits and this line was named the Botucatu (Moura *et al.*, 2001). In Egypt, a multi-purpose selection program was started in March 2003 to produce a synthetic line (named Moshtohor), resulting from crossing Sinai Gabali with V-line and selection was practiced for litter weight at weaning and live weight at 56 days (Iraqi *et al.*, 2007, 2008).

Direct and correlated selection responses

Estimates of direct and correlated selection responses obtained from selection experiments are presented in Table 6. Lines selected based on different objectives showed that selection for growth rate have a better feed efficiency than selection for reproductive traits (Torres *et al.*, 1992; Feki *et al.*, 1996).

Table 6: Direct and/or correlated selection response per generation obtained from multi-purpose selection experiments

Authors	Breed or line	Selection criteria	Methodology	Direct and/or correlated selection responses per generation [†]
Moura <i>et al.</i> (1997)	Composite population	Daily gain + feed conversion (28-70 d)	Genetic trend in divergent selection program using BLUP	ADG = 1.23 g per d; FCI = -0.20 g feed per g gain
Gómez <i>et al.</i> (2000)	Caldes line	LWW + ADG (32-60 d)	Annual genetic trends using BLUP	LSB = 0.0 rabbits per litter; LSW = 0.03 rabbits per litter; LWW=30.7 g per litter; ADG = 1.06 g/d; WW = 11 g per rabbit; W60 = 38 g per rabbit
Moura <i>et al.</i> (2001)	Botucato	LSW, WW, LWW, 70-d weight	Genetic trend in multiple-trait selection using mixed-model methodology	NBA = 0.034 rabbits per litter; LSW = 0.039 rabbits per litter; LWW = 35.2 g per litter; WW= 6.74 g per rabbit; W70 = 17.2 g per rabbit

[†]LSB: litter size at birth; NBA: number born alive; LSW: litter size at weaning; LWW: litter weight at weaning; WW: weaning weight; W60: weight at 60 days; W70: weight at 70 days; ADG: average daily gain; FCI: feed conversion index.

In Spain, selection responses obtained from selecting for litter size at weaning and daily weight gain in the Caldes line (Gómez *et al.*, 2000) are summarized in Table 6 that indicates: (1) direct response for litter size at weaning was 0.03 rabbits per litter, while indirect responses for litter weight at weaning, and individual weight at weaning were 30.7 g per litter and 11 g per rabbit per year, respectively; (2) direct response for daily gain was around 1.06 g per day, with an indirect response of 38 g per rabbit per year for individual weight at 60 days; (3) ability of the doe to raise her litter was also improved because genetic response for litter size at weaning was higher than the response for litter size at birth; (4) selection for litter weight at 60 days achieved positive responses for growth rate, while maintaining high reproductive performances; (5) selection for a total objective has achieved responses for growth traits without impairment of litter size at weaning.

Salaün *et al.* (2001) in France stated that annual genetic gain for selecting litter weight at weaning was 342 g, which was equal to 1.7% of the phenotypic mean or 3.2% of the phenotypic standard deviation. In Brazil, Moura *et al.* (2001) reported that the annual genetic gain for litter size at weaning, weaning litter weight and 70-d market weight in multi-purpose selection program were 0.04 rabbits per litter, 35.2 g per litter, and 17.2 g per rabbit, respectively.

DIRECT AND INDIRECT SELECTION FOR WOOL TRAITS

In the literature, results dealing with selection experiments for wool traits in Angora rabbits are very limited (Rafat *et al.*, 2007).

Selection criteria and methods

Selection for total fleece weight was successfully performed in French Angora rabbits (Rochambeau *et al.*, 2000; Allain *et al.*, 2004; Rafat *et al.*, 2007, 2008). However, it is unclear whether or not high fleece weight is associated with an increase in other fleece characteristics (length, diameter, compression and secondary to primary follicle ratio) in Angora rabbits. Nonetheless, selection for total fleece weight is a simple and easy criterion to measure, and it is very efficient to improve weight of 1st class quality wool, which is an important economic trait in French Angora wool production.

Direct and correlated selection responses

In order to estimate direct and correlated selection responses for wool production and other wool quality traits, an 8-year divergent selection experiment was carried out on French Angora rabbits based on selection for total fleece weight (Rafat *et al.*, 2007, 2008). Results obtained in this experiment indicated that: (1) response in total fleece weight was substantial with an annual divergence rate between the high and low lines in mean breeding values to be 80.95 g or 3.04 genetic standard deviations; (2) correlated responses in other fleece quality traits were significant with divergence rates of 2.96, 2.78 and 1.21 genetic standard deviations for weight of 1st class quality wool (W1), weight of 2nd class quality wool (W2), and wool homogeneity (the ratio of W1 to total fleece weight), respectively; (3) live body weight increased significantly by selection for total fleece weight; (4) a positive divergence rate of 0.92 genetic standard deviations between the two selection lines was observed for bristle length, while negative divergence rates of 1.00, 1.31, 0.38 and 0.50 genetic standard deviations were observed for compression, resilience, bristle diameter and fiber diameter, respectively.

Allain *et al.* (2004) reported that direct selection for fleece weight in long Angora rabbits was associated by positive divergence rates of 3.0, 0.7 and 0.9 genetic standard deviations for fleece weight, fleece homogeneity and bristle length, respectively, while negative divergence rates of 0.9, 0.9, 1.1 and 0.4 genetic standard deviations were observed for lock structure, compression, resilience and live body weight, respectively. No other results on correlated selection responses for total fleece weight or for fleece characteristics in Angora rabbits have been published. Similar to the results of Angora rabbits, Bai *et al.* (2006) suggested that selection for cashmere weight in goats was very effective, which has led to slow genetic progress in fibre length due to its negative genetic correlation with cashmere weight. In another study, Redden *et al.* (2005) concluded that selection for increased cashmere weight results in a reduction in quality and value of the fleece.

CONCLUSIONS AND FUTURE PROSPECTS

- 1) In developed countries, specialized maternal or paternal lines were mostly developed for use on commercial farms, while in developing countries the synthesis of multi-purpose lines are necessary for use in national breeding programmes for the rabbit industry.
- 2) Spanish V-line rabbits genetically selected for more than 35 generations have been introduced in various countries (as live animals or as frozen embryos) using recent bio-techniques and applying selection and/or crossbreeding with local lines. This line has been widely distributed in some countries of the world, such as France, Egypt, Saudi Arabia, Turkey, and Uruguay.
- 3) Direct selection has had little or moderate effects on litter size, prenatal litter components, and meat quality traits, while it has had major effects on post weaning growth and carcass traits, feed conversion, and fleece weight in Angora rabbits. Direct selection for feed efficiency is less efficient than selection for growth rate for improving feed conversion ratio.
- 4) Selection for increasing total fleece weight has resulted in beneficial effects on other fleece quality traits and on live body weights in Angora rabbits. Detecting QTL and major genes for hair follicle production are considered to be a valuable tool for selection programs of selection in Angora rabbits (Allain *et al.*, 2004).
- 5) New techniques, such as laparoscopy, ovariectomization, cryopreservation of embryos and semen, TOBEC (Total Body Electrical Conductivity), and X-ray scanning computerized tomography (CT), have been introduced successfully as tools to assist in selection programs. Selection based on the X-ray computerized tomography measurement could be effective to improve carcass traits in rabbits.

- 6) Results of available molecular techniques are not presently of sufficient accuracy to be used in selection programs in rabbits; although the Spanish and French teams have verified the hypothesis that there are major genes affecting components of litter size, uterine capacity and ovulation rate. A genetic map with microsatellite markers distributed every 10 to 20 cM along the rabbit genome is available as stated by Chantry-Darmon *et al.* (2004). This breakthrough will help to efficiently construct linkage maps, based on molecular markers for use in selection programs. Simultaneously, the corresponding cytogenetic maps were established in order to provide the chromosomal position of all the genetic markers.
- 7) To date, marker-assisted selection (MAS) is not generally used in current rabbit selection programs, and the recent molecular technologies were used only to identify genetic diversity, gene mapping and DNA fingerprinting in different breeds of rabbits.
- 8) As to future prospects, localizing loci of genes of economic interest are necessary to identify the candidate animals in selection programs and to elucidate the molecular nature of the few already verified major genes.

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