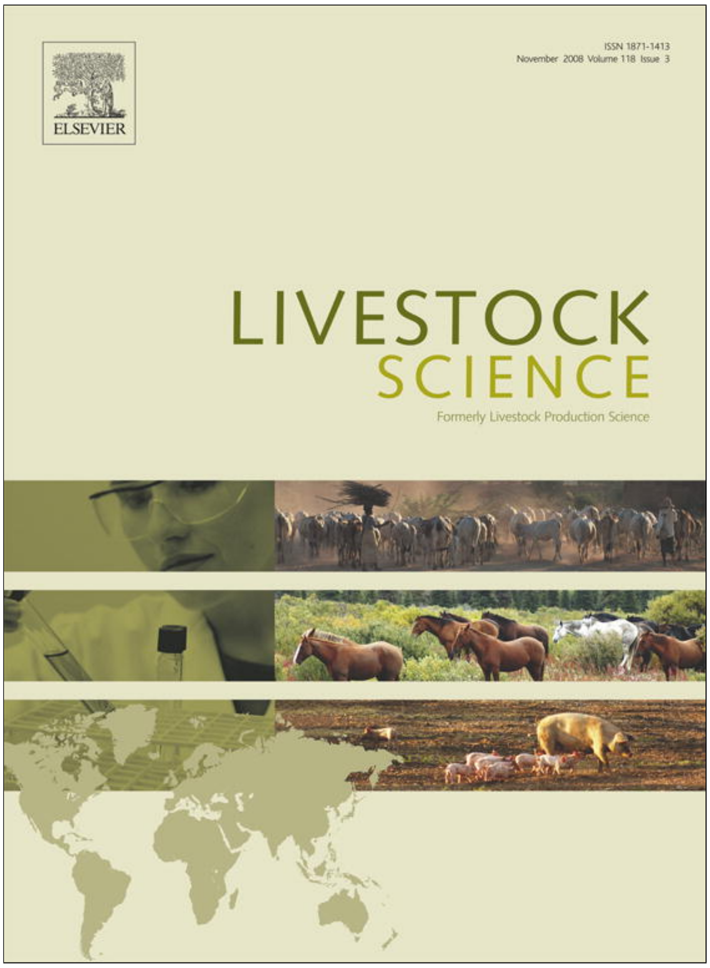
ISSN 1871-1413
November 2008 Volume 118 Issue 3
ELSEVIER
LIVESTOCK
SCIENCE
Formerly Livestock Production Science

Available online at www.sciencedirect.com
ScienceDirect

Livestock Science 118 (2008) 238–246

LIVESTOCK SCIENCE

www.elsevier.com/locate/livsci

Crossbreeding effects for litter and lactation traits in a Saudi project to develop new lines of rabbits suitable for hot climates

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Received 11 September 2007; received in revised form 27 January 2008; accepted 30 January 2008

Abstract

A five-years crossing scheme involving the Spanish V line (V) and Saudi Gabali (S) rabbits was practiced to produce 14 genetic groups: V, S, 1/2V1/2S, 1/2S1/2V, 3/4V1/4S, 3/4S1/4V, $(1/2V1/2S)^2$, $(1/2S1/2V)^2$, $(3/4V1/4S)^2$, $(3/4S1/4V)^2$, $((3/4V1/4S)^2)^2$, $((3/4S1/4V)^2)^2$, Saudi 2 (a new synthetic line) and Saudi 3 (another new synthetic line). A total of 3496 litters from 1022 dams were used to evaluate litter size at birth (LSB) and weaning (LSW), litter weight at birth (LWB), litter weight at 21 d (LW21) and litter weight at weaning (LWW), pre-weaning litter mortality (PLM), milk yield at lactation intervals of 0–7 d (MY07), 0–21 d (MY021), 0–28 d (TMY) and milk conversion ratio as g of litter gain per g of milk suckled during 21 d of lactation (MCR021). A generalized least squares procedure was used to estimate additive and heterotic effects (direct, maternal, and grand-maternal).

The comparison among V, S, Saudi 2 and Saudi 3 showed a complementarity between V and S. Line V was superior for LSB, LSW, LWB, PLM, MY07, MY021 and TMY, while line S was superior for the other traits (LW21, LWW and MCR021). Saudi 2 and Saudi 3 had the means equal to or higher than the founder lines (V or S) for all traits. Saudi 2 showed better values in litter size and pre-weaning litter mortality compared to Saudi 3 with no significant differences for the other traits. Concerning crossbreeding parameters, direct additive effects were significant for all traits, ranging between 12.3% and 31.8% relative to the average of the means of V and S. All estimates for direct heterosis except LWB and MCR021 were significant and ranged from 5.3% to 27.5%. No estimates for maternal additive effects and grand-maternal additive and heterotic effects were significant. Only estimates for maternal heterotic effects of LSB and LSW were significant (8.6% and 10.6%, respectively).

Keywords: Rabbits; Crossbreeding; Synthetic lines; Litter traits; Lactation; Additive effects; Heterosis

1. Introduction

In the last two decades, some developing countries have been interested in increasing their rabbit meat production through carrying out selection programs based on local breeds and exotic lines (Garreau et al.,

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doi:10.1016/j.livsci.2008.01.025

2004). In hot-climate countries, such as Saudi Arabia and Egypt, selection programs for meat rabbits are currently active, addressing different issues under a broad perspective taking into account the adaptation to the heat (El-Raffa et al., 2005). The main point of these programs is dealing with the constitution and definition of the breeds and lines on which the selection and the production are to be based. Thus, the scheme followed in Saudi Arabia and Egypt has similar bases depending on the local breeds or using an exotic line selected for prolificacy that performs well under hot conditions (García and Baselga, 2002; Khalil et al., 2002) and synthetic lines between the local breeds and the exotic lines. The small-scale producers are the main beneficiaries of these new synthetics lines.

During the process of synthesizing new lines, it is common that several genetic types of animals, like the founders, F_1, F_2, backcrosses, other types of crossbreds and synthetics, perform contemporarily allowing a connection between all of them. This fact permits, if an adequate recording system is maintained along the process, a joint analysis of their records and estimates of many crossbreeding parameters between the founder breeds or lines of the synthetics (Dickerson, 1973), depending on the depth of the analysis for the number available in different types of animals. The knowledge of these parameters is useful to explain the differences between the founders and the synthetics and it also permits the prediction of the performance of other types of crosses among them. In Saudi Arabia, the procedure followed to create two new synthetic lines had three important requirements (Khalil et al., 2005): (1) connection among genetic groups, (2) adequate recording system, and (3) high number of genetic groups.

Traits related to productivity of the does, such as litter size, litter weight, milk production and longevity are considered the most important traits for efficient production and some of these traits are objectives of selection to develop maternal lines of rabbits (Estany et al., 1989; Gómez et al., 1996; de Rochambeau et al., 1998; Baselga, 2004). A deep knowledge involving crossbreeding parameters for these traits is lacking in temperate areas (Baselga et al., 2003; Brun and Baselga, 2005) and in hot climates (Khalil and Afifi, 2000; Khalil et al., 1995, 2004, 2005). Thus, the objectives of the present study were: (1) to evaluate the results of two new lines of rabbits, and (2) to estimate the crossbreeding parameters for litter and milk traits in terms of additive and heterotic effects (direct, maternal, and grand-maternal), recombination losses and cyto-plasmatic effects in a crossbreeding program involving one Saudi breed and one exotic line of rabbits, that are the founders of the new lines.

2. Materials and methods

2.1. Animals and crossbreeding program

A five-year crossbreeding project involving the desert Saudi Gabali breed (S) and the Spanish V line (V) was started in September 2000 in the experimental rabbitry, College of Agriculture and Veterinary Medicine, El-Qassim region to develop two new lines of rabbits in Saudi Arabia. Eighty pedigreed dams and sixteen pedigreed sires of V line rabbits were imported from Universidad Politécnica de Valencia, Spain, in September 2000. The V line is a maternal rabbit line selected for number of young weaned per litter (Estany et al., 1989) for 21 generations, while S line is a Saudi breed raised under desert conditions, especially in the Najd area. Rabbits of this breed are characterized by litter size of 6–8 young, mature body weight of 3200–3800 g and the ability to survive and adapt to produce and reproduce under hot environments. Before the starting of our program, no selection program was practiced in this breed and it has not originated from any crossbreeding program.

Two parallel crossbreeding schemes were carried out. The first scheme began by crossing S sires and V line dams to get the F_1 (1/2S1/2V), then dams and sires of this F_1 were mated to get the F_2 $(1/2S1/2V)^2$ and at the same time dams of F_1 were backcrossed with sires of V line to get 3/4V1/4S, then progeny of the backcross were mated to get $(3/4V1/4S)^2$, followed by one generation of *inter se* mating to get $((3/4V1/4S)^2)^2$ and finally three generations of inter se mating of the previous progeny was practiced to get a new synthetic maternal line named Saudi 2. The second scheme began by crossing V line sires with Saudi dams to get the F_1 cross (1/2V1/2S), then dams and sires of this F_1 were mated to get the F_2 $(1/2V1/2S)^2$ and at the same time dams of F_1 were backcrossed with Saudi sires to get 3/4S1/4V, then progeny of this backcross were mated to get $(3/4S1/4V)^2$, followed by one generation of *inter se* mating to get $((3/4S1/4V)^2)^2$ and finally three generations of inter se mating of the previous progeny was practiced to get a new synthetic line named Saudi 3. The breeding plan in the project permitted connected production of 14 genetic groups as shown in Table 1. The sires were randomly assigned to mate the dams naturally with the restriction to avoid the matings of animals with common grandparents. A total of 3496 litters of 1022 dams were used. These dams were obtained by crossing 419 dams and 151 sires. Numbers of litters born in V, S, 1/2V1/2S, 1/2S1/2V, 3/4V1/4S, 3/4S1/4V, $(1/2V1/2S)^2$, $(1/2S1/2V)^2$, $(3/4V1/4S)^2$, $(3/4S1/4V)^2$, $((3/4V1/4S)^2)^2$, $((3/4S1/4V)^2)^2$, Saudi 2, and Saudi 3 lines were 753, 571, 264, 280, 122, 277, 37, 77, 222, 164, 89, 187, 149 and 304, respectively.

2.2. Housing and feeding

Rabbits were raised in a semi-closed rabbitry. Breeding dams and sires were housed separately in individual wire cages. All cages were equipped with feeding hoppers and drinking nipples. In the rabbitry, the environmental conditions were monitored; temperature ranged from 20 °C to about

Table 1
Genetic group of the dams, their parents and grand dams

Genetic group				Mean	Direct effect				Maternal effect			Grand-maternal effect			Cytoplasmic effect	
Dam	Sire	Dam	Grand dam	μ	D_V	D_S	H^I	R^I	M_V	M_S	H^M	GM_V	GM_S	H^{GM}	C_V	C_S
V-line (V)	V	V	V	1	1	0	0	0	1	0	0	1	0	0	1	0
Saudi Gabali (S)	S	S	S	1	0	1	0	0	0	1	0	0	1	0	0	1
1/2V1/2S	V	S	S	1	0.5	0.5	1	0	0	1	0	0	1	0	0	1
1/2S1/2V	S	V	V	1	0.5	0.5	1	0	1	0	0	1	0	0	1	0
3/4V1/4S	V	1/2S1/2V	V	1	0.75	0.25	0.5	0.25	0.5	0.5	1	1	0	0	1	0
3/4S1/4V	S	1/2V1/2S	S	1	0.25	0.75	0.5	0.25	0.5	0.5	1	0	1	0	0	1
$(1/2V1/2S)^2$	1/2V1/2S	1/2V1/2S	S	1	0.5	0.5	0.5	0.5	0.5	0.5	1	0	1	0	0	1
$(1/2S1/2V)^2$	1/2S1/2V	1/2S1/2V	V	1	0.5	0.5	0.5	0.5	0.5	0.5	1	1	0	0	1	0
$(3/4V1/4S)^2$	3/4V1/4S	3/4V1/4S	1/2S1/2V	1	0.75	0.25	0.375	0.375	0.75	0.25	0.5	0.5	0.5	1	1	0
$(3/4S1/4V)^2$	3/4S1/4V	3/4S1/4V	1/2V1/2S	1	0.25	0.75	0.375	0.375	0.25	0.75	0.5	0.5	0.5	1	0	1
$((3/4V1/4S)^2)^2$	$(3/4V1/4S)^2$	$(3/4V1/4S)^2$	3/4V1/4S	1	0.75	0.25	0.375	0.375	0.75	0.25	0.375	0.75	0.25	0.5	1	0
$((3/4S1/4V)^2)^2$	$(3/4S1/4V)^2$	$(3/4S1/4V)^2$	3/4S1/4V	1	0.25	0.75	0.375	0.375	0.25	0.75	0.375	0.25	0.75	0.5	0	1
Saudi 2	$((3/4V1/4S)^2)^2$	$((3/4V1/4S)^2)^2$	$(3/4V1/4S)^2$	1	0.75	0.25	0.375	0.375	0.75	0.25	0.375	0.75	0.25	0.375	1	0
Saudi 3	$((3/4S1/4V)^2)^2$	$((3/4S1/4V)^2)^2$	$(3/4S1/4V)^2$	1	0.25	0.75	0.375	0.375	0.25	0.75	0.375	0.25	0.75	0.375	0	1

Coefficients of the matrix which relate the genetic means of the dams with the crossbreeding parameters.
$D_V(D_S)$, $M_V(M_S)$, and $GM_V(GM_S)$ = Direct, maternal, and grand-maternal additive genetic effects for V-line (Saudi Gabali breed), respectively; H^I, H^M and H^{GM} = Direct, maternal and grand-maternal heterosis, respectively; R^I = recombination losses; $C_V(C_S)$ = Cytoplasmatic effects for V-line (Saudi Gabali breed).

32 °C, the relative humidity ranged from 20% to 50% and photoperiod was 16L:8D. Young rabbits were weaned at four weeks of age. Rabbits were fed a commercial pelleted diet during the whole period. On a dry matter basis, the diet contained 17.9% crude protein, 15.57% crude fiber, 2.45% ether extract, 58.5 nitrogen free extract, and 6.29% ash. Feed and water were available *ad libitum*.

2.3. Data collected

The milk yield of does was recorded at 7, 21 and 28 d of lactation, using the weigh-suckle-weigh method described by Lukefahr et al. (1983b) and Khalil (1994). The young rabbits were separated from their dams in the evening to prevent suckling for a period of 12 h. The kits and the dam were weighed in the morning and then placed in the nest box of the doe's cage. Usually, the doe immediately entered the box, nursed the litter and left within 3 to 5 min. The litter and the dam were removed promptly, reweighed separately and returned to the nest box and cage, respectively. In order to avoid a biased estimate of milk yield (e.g., in case the kits or the does urinated), we used both weights and the milk yield of the doe was estimated by the average difference between the pre- and post-suckling litter and doe weight.

Data collected were litter size at birth (LSB, young) and weaning (LSW, young), litter weight at birth (LWB, g), litter weight at 21 d (LW21, g) and at weaning (LWW, g), pre-weaning litter mortality (PLM, %), milk yield at lactation intervals of 0–7 d (MY07, g), 0–21 d (MY021, g), 0–28 d (TMY, g), and milk conversion ratio as g of litter gain per g of milk suckled during 21 d of lactation (MCR021, g/g).

2.4. Model of analysis and estimation of crossbreeding genetic parameters

A single-trait animal model was used for all traits. This model was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a u_a} + \mathbf{Z_p u_p} + \mathbf{e}$$

where **y** was the vector of records of the trait, **b** was the vector of fixed effects of genetic groups of the doe (14 levels; see Table 1), year-season of kindling (one year season every three months), and parity order of the doe (five levels); $\mathbf{u_a}$ was the vector of random additive effects of the dams and sires in the pedigree, $\mathbf{u_p}$ was the vector of random effects of the permanent environment of the doe (permanent non-additive effect); **X**, $\mathbf{Z_a}$ and $\mathbf{Z_p}$ were the incidence matrices relating records to the fixed effects, additive genetic effects, and permanent environment, respectively; and e was the vector of random residual effects.

Variance components of the random effects were estimated by a derivate-free restricted maximum likelihood procedure using MTDFREML software of Boldmann et al. (1995). These variance components were used to solve the corresponding mixed model equations, obtaining solutions for the genetic group means and their error variance–covariance matrix, using the PEST (Groenoveld, 1990). To get the estimates of the crossbreeding genetic parameters of the lines (Dickerson, 1973), a procedure of generalized least squares (GLS) was applied (Baselga et al., 2003). The following linear model was used:

$$\mathbf{y} = \mathbf{X}b + \mathbf{e},\ \ \mathrm{Var}(\mathbf{y}) = \mathbf{V}$$

where **y** was the vector of estimated group means from the animal model, using the S line as a reference group; **X** was an incidence matrix, **b** was the vector of estimable crossbreeding genetic parameters, **e** was the vector of residual effects, and **V** was the error variance–covariance matrix of **y**, from the animal model. The coefficients relating genetic crossbreeding parameters to the means of the genetic groups are showed in Table 1 (Dickerson, 1992; Wolf et al., 1995). The estimable crossbreeding parameters are the differences between direct genetic effects ($D = D_V - D_S$), between maternal genetic effects ($M = M_V - M_S$), between grand-maternal genetic effects ($GM = GM_V - GM_S$) and between cytoplasmic effects ($C = C_V - C_S$); the direct (H^{I}), maternal (H^{M}), and grand-maternal (H^{GM}) heterosis and the recombination losses (R^{I}) (Baselga et al., 2003). Thus, we have eight parameters to estimate, components of **b:**

$$\mathbf{b}' = \left[D \quad H^{\mathrm{I}} \quad R^{\mathrm{I}} \quad M \quad H^{\mathrm{M}} \quad \mathrm{GM} \quad H^{\mathrm{GM}} \quad C\right]$$

The estimates of ***b*** calculated by generalized least squares (GLS) were given by the equation:

$$\hat{b} = \left(X' V^{-} X\right)^{-1} X' V^{-} y$$

where **X** was the matrix of coefficients of estimable crossbreeding effects, coming from Table 1, after subtracting from each row the row of group 2 (S line), being:

$$\left[\begin{array}{cccccccc}
D & H^{\mathrm{I}} & R^{\mathrm{I}} & M & H^{\mathrm{M}} & \mathrm{GM} & H^{\mathrm{GM}} & C \\
1.0 & 0.0 & 0.0 & 1.0 & 0.0 & 1.0 & 0.0 & 1.0 \\
0.0 & 0.0 & 0.0 & 0.0 & 0.0 & 0.0 & 0.0 & 0.0 \\
0.5 & 1.0 & 0.0 & 0.0 & 0.0 & 0.0 & 0.0 & 0.0 \\
0.5 & 1.0 & 0.0 & 1.0 & 0.0 & 1.0 & 0.0 & 1.0 \\
0.75 & 0.5 & 0.25 & 0.5 & 1.0 & 1.0 & 0.0 & 1.0 \\
0.25 & 0.5 & 0.25 & 0.5 & 1.0 & 0.0 & 0.0 & 0.0 \\
0.5 & 0.5 & 0.5 & 0.5 & 1.0 & 0.0 & 0.0 & 0.0 \\
0.5 & 0.5 & 0.5 & 0.5 & 1.0 & 1.0 & 0.0 & 1.0 \\
0.75 & 0.375 & 0.375 & 0.75 & 0.5 & 0.5 & 1.0 & 1.0 \\
0.25 & 0.375 & 0.375 & 0.25 & 0.5 & 0.5 & 1.0 & 0.0 \\
0.75 & 0.375 & 0.375 & 0.75 & 0.375 & 0.75 & 0.5 & 1.0 \\
0.25 & 0.375 & 0.375 & 0.25 & 0.375 & 0.25 & 0.5 & 0.0 \\
0.75 & 0.375 & 0.375 & 0.75 & 0.375 & 0.75 & 0.375 & 1.0 \\
0.25 & 0.375 & 0.375 & 0.25 & 0.375 & 0.25 & 0.375 & 0.0
\end{array}\right]$$

with the variance–covariance matrix of the estimate of ***b*** being,

$$\mathrm{Var}\left(\hat{\mathbf{b}}\right) = \left(\mathbf{X}' \mathbf{V}^{-} \mathbf{X}\right)^{-1}$$

This matrix was used to test the significance of the crossbreeding effects. All statistical tests were done at $\alpha = 0.05$.

The main objective of this study was to estimate the crossbreeding parameters in terms of additive and heterotic effects (direct, maternal, and grand-maternal), recombination losses and cytoplasmic effects. Estimation of these crossbreeding parameters was carried out using the above methodology. Some unexpected estimates were obtained, for example, the effects of recombination losses and cytoplasmic inheritance for some traits were similar or had higher values than the additive direct effects. Particularly, the structure of our data was not well conditioned to estimate the recombination losses since the standard errors of these estimates were three times the standard errors of the estimates of the other parameters. The methodology proposed to estimate the crossbreeding parameters was used to fit 13 estimable functions of the genetic group effects through eight estimable functions of the crossbreeding parameters. As a result, the degrees of freedom for the error were only five and the model became very sensitive to the random effects affecting the genetic group estimates. For these reasons, the model of crossbreeding parameters was simplified by eliminating the effects of recombination losses and the cytoplasmic inheritance. Accordingly, the columns corresponding to these effects in Table 1 and matrix **X** relating crossbreeding parameters to genetic groups were eliminated. Consequently, the results reported here refer to the estimates obtained using such a simplified model.

3. Results and discussion

3.1. Overall actual means and variation

Means, standard deviations and minimum and maximum values for litter and lactation traits are presented in Table 2. In hot countries, slightly lower values were

Table 2
Summary statistics for litter and milk traits

Doe trait	No.	Mean	Standard Deviation	Minimum	Maximum
Litter traits[a]:					
LSB (young)	3496	9.26	2.39	1	17
LSW (young)	3409	7.69	3.10	1	15
LWB (g)	3496	438	139	25	825
LW21 (g)	3416	1748	675	240	4568
LWW (g)	3398	3370	1457	360	9580
PLM (%)	2762	20.8	4.9	0	100
Milk traits[b]:					
MY07 (g)	3435	1060	433	150	3483
MY021 (g)	3435	3776	1401	350	11,849
TMY (g)	3413	4826	1697	1290	14,898
MCR021 (g/g)	3413	0.356	0.157	0.020	1.560

[a] LSB = Litter size at birth; LSW = Litter size at weaning; LWB = litter weight at birth; LW21 = Litter weight at 21 d; LWW = Litter weight at weaning; PLM = Pre-weaning litter mortality.

[b] Milk yield at lactation intervals of 0–7 d (MY07); 0–21 d (MY021); and 0–28 d (TMY); MCR021 = Milk conversion ratio as g of litter gain per g of milk suckled during 21 d of lactation.

reported by Ayyat et al. (1995) and Khalil and Afifi (2000) and much lower values by Khalil (1994) and Abd El-Aziz et al. (2002). Consequently, these results are positive for rabbit production in the Arabian Gulf countries and show the potential to involve the V line in crossbreeding programs in this area and in other hot climatic areas. However, means obtained in the present study are nearly similar to those reported in more temperate areas such as the US (Lukefahr et al., 1983a,b, 1996), Denmark (Sorensen et al., 2001), Spain (Gómez et al., 1996; García et al., 2000b), or Latin America (Capra et al., 2000; Moura et al., 2001).

3.2. Additive and non-additive genetic and permanent environmental effects

The proportion of the phenotypic variance due to genetic additive effects, permanent environmental and non-additive effects and random error are given in Table 3.

Heritabilities for litter and milk traits were mostly low or moderate, ranging from 0.03 to 0.17 for litter traits and from 0.07 to 0.15 for milk traits (Table 3). Estimates of heritability obtained in the present study for litter and milk traits are within the ranges found in the literature estimated by animal models (Ferraz et al., 1992; Lukefahr and Hamilton, 1997; Rastogi et al., 2000; Sorensen et al., 2001; Al-Sobayil et al., 2005; El-Deghady, 2005; Khalil et al., 2005).

Table 3
Estimates of the proportion of the phenotypic variance due to genetic additive effects (h^2), to non-additive and permanent environmental effects (p^2) and to error (e^2) with their standard errors (±s.e.) for litter and lactation traits

Doe trait	h^2±s.e.	p^2±s.e.	e^2±s.e.
Litter traits [a]:			
LSB (young)	0.04±0.009	0.18±0.019	0.78±0.019
LSW (young)	0.05±0.021	0.11±0.024	0.84±0.019
LWB (g)	0.15±0.021	0.14±0.03	0.71±0.019
LW21 (g)	0.17±0.018	0.11±0.003	0.73±0.017
LWW (g)	0.15±0.003	0.10±0.003	0.75±0.002
PLM (%)	0.03±0.018	0.18±0.023	0.79±0.018
Milk traits [b]:			
MY07 (g)	0.07±0.023	0.07±0.024	0.86±0.018
MY021 (g)	0.15±0.001	0.09±0.001	0.75±0.001
TMY (g)	0.15±0.001	0.11±0.001	0.74±0.001
MCR021 (g/g)	0.13±0.017	0.05±0.019	0.72±0.015

[a] LSB = Litter size at birth; LSW = Litter size at weaning; LWB = litter weight at birth; LW21 = Litter weight at 21 d; LWW = Litter weight at weaning; PLM = Pre-weaning litter mortality.

[b] Milk yield at lactation intervals of 0–7 d (MY07); 0–21 d (MY021); and 0–28 d (TMY); MCR021 = Milk conversion ratio as g of litter gain per g of milk suckled during 21 d of lactation.

Table 4
Estimates and standard error of the differences of the effects of lines V, Saudi 2 and Saudi 3 relative to Saudi Gabali (S) breed for litter and lactation traits

Doe trait	Line V *vs.* line S	Saudi 2 *vs.* line S	Saudi 3 *vs.* line S
Litter traits [a]:			
LSB (young)	1.82±0.21 *	2.96±0.40 *	2.26±0.36 *
LSW (young)	2.34±0.27 *	4.41±0.50 *	2.82±0.46 *
LWB (g)	91.1±15.0 *	150.7±26.4 *	150.1±24.5 *
LW21 (g)	−303±77 *	−90±133	−123±124
LWW (g)	−506±160 *	−105±281	−299±261
PLM (%)	−10.7±2.0 *	−22.7±3.8 *	−12.7±3.5 *
Milk traits [b]:			
MY07 (g)	269±38 *	191±71 *	130±65 *
MY021 (g)	553±152 *	305±266	197±247
TMY (g)	710±187 *	470±328	221±305
MCR021 (g/g)	−0.066±0.016 *	−0.036±0.029	−0.041±0.026

[a] LSB = Litter size at birth; LSW = Litter size at weaning; LWB = litter weight at birth; LW21 = Litter weight at 21 d; LWW = Litter weight at weaning; PLM = Pre-weaning litter mortality.

[b] Milk yield at lactation intervals of 0–7 d (MY07); 0–21 d (MY021); and 0–28 d (TMY); MCR021 = Milk conversion ratio as g of litter gain per g of milk suckled during 21 d of lactation.

* $P<0.05$.

The ratios of permanent environmental effects were mostly moderate and ranged from 0.10 to 0.18 for litter traits, while these ratios were low and ranged from 0.05 to 0.11 for milk traits. Similar estimates have been reported by other authors, using the same methodology (Lukefahr and Hamilton, 1997; El-Raffa, 2000; Sorensen et al., 2001; Al-Sobayil et al., 2005; El-Deghady, 2005; Khalil et al., 2005).

3.3. Differences among the lines V, Saudi Gabali, Saudi 2 and Saudi 3 for genetic group effects

In order to evaluate the results of the two synthesized lines (Saudi 2 and Saudi 3), a comparison between these lines and line V and S was carried out. Tables 4 and 5 show the results of the tests of differences between all of them obtained from the solutions of the mixed model equations for genetic group effects.

The comparison between line V and S showed a very clear pattern of complementarity between both lines. They were significantly different for all traits studied. Line V was superior in LSB (1.82 young), LSW (2.34 young), LWB (91.1 g), PLM (−10.7%) and milk yield, but LW21 (−303 g), LWW (−506 g) and MCR021 (−0.066 g/g) were in favour of line S. The superiority of line V in litter size traits is in agreement with its long history of selection for litter size at weaning (Baselga, 2004). The line V has shown this superiority in other

Table 5
Estimates and standard error of differences of the effects of Saudi 2 and Saudi 3 lines relative to line V, and Saudi 3 relative to Saudi 2 for litter and lactation traits

Doe trait	Saudi 2 *vs* line V	Saudi 3 *vs* line V	Saudi 3 *vs* Saudi 2
Litter traits [a]:			
LSB (young)	1.14±0.39*	0.44±0.38	−0.70±0.35*
LSW (young)	2.07±0.48*	0.48±0.43	−1.60±0.43*
LWB (g)	59.6±25.4*	59.0±23.5*	−0.6±23.8
LW21 (g)	213±127	180±118	−33±119
LWW (g)	401±266	207±248	−193±248
PLM (%)	−12.0±3.7*	−1.9±3.3	10.1±3.3*
Milk traits [b]:			
MY07 (g)	−79±68	−139±62*	−60±62
MY021 (g)	−249±254	−357±236	−108±238
TMY (g)	−240±311	−489±289	−249±290
MCR021 (g/g)	0.030±0.027	0.025±0.025	−0.004±0.025

[a] LSB = Litter size at birth; LSW = Litter size at weaning; LWB = litter weight at birth; LW21 = Litter weight at 21 d; LWW = Litter weight at weaning; PLM = Pre-weaning litter mortality.

[b] Milk yield at lactation intervals of 0–7 d (MY07); 0–21 d (MY021); and 0–28 d (TMY); MCR021 = Milk conversion ratio as g of litter gain per g of milk suckled during 21 d of lactation.

* $P<0.05$.

experiments carried out in hot climates (Yamani, 1994; Testik, 1996; El-Raffa, 2000). Better MCR021, LW21 and LWW for the line S could be interpreted on the basis that this breed is more adaptable to the hot environment from which it comes than line V.

Just as with line V, Saudi 2 and Saudi 3 were superior to line S in LSB, LSW, PLM and MY07 but not significantly different for the other milk traits (Table 4). Relative to line V, Saudi 2 with 3/4 of its genes coming from line V, was also superior in LSB (1.14 young), LSW (2.07 young), LWB (59.6 g) and PLM (−12.0%) and not significantly different for the other traits (Table 5). Also, Saudi 3 with only 1/4 of its genes coming from line V showed significantly higher values for LWB (59.0 g) and significantly lower values for MY07 (−139 g) than line V, but the differences between the lines were non-significant for the other traits.

Comparing Saudi 3 with Saudi 2, the latter showed better values in LSB (−0.70 young), LSW (−1.60) and PLM (10.1%) with no significant differences for the other traits. Results from the two synthetic lines developed in the present study have shown equal or superior performance in the studied traits relative to the founder lines. Saudi 2 seems more promising than Saudi 3 as a specialised maternal line since it shows better LSB and LSW associated with lower PLM.

3.4. Direct, maternal and grand-maternal additive effects

Table 6 shows the differences between lines V and S in terms of direct, maternal and grand-maternal additive effects. The differences in direct additive effects between the two lines were significant for all studied traits, but the estimates of maternal and grand-maternal

Table 6
Estimates of differences between line V and Saudi Gabali breed in direct, maternal and grand-maternal additive effects and their standard errors (±s.e.) for litter and lactation traits

Doe trait	Direct additive effects		Maternal additive effects		Grand-maternal additive effects	
	Estimate±s.e.	% [c]	Estimate±s.e.	%	Estimate±s.e.	%
Litter traits [a]:						
LSB (young)	1.41±0.34*	16.5	0.24±0.34	2.8	−0.10±0.30	−1.2
LSW (young)	1.71±0.41*	24.9	0.16±0.40	2.3	0.10±0.36	1.5
LWB (g)	50.7±21.8*	12.3	6.3±20.3	1.5	10.3±18.4	2.5
LW21 (g)	−283±107*	−18.5	−37±98	−2.4	24±89	1.6
LWW (g)	−460±225*	−15.5	−80±208	−2.7	57±188	1.9
PLM (%)	−6.6±3.2 *	−31.8	−0.4±3.2	−1.9	−2.0±2.8	−9.6
Milk traits [b]:						
MY07 (g)	191±58*	21.7	78±56	8.9	−62±50	−7.0
MY021 (g)	560±215*	18.1	186±198	6.0	−302±180	−9.7
TMY (g)	763±264*	19.7	230±243	5.9	−435±221	−11.3
MCR021 (g/g)	−0.070±0.023*	−22.5	−0.009±0.021	−3.0	−0.018±0.019	−6.0

[a] LSB = Litter size at birth; LSW = Litter size at weaning; LWB = litter weight at birth; LW21 = Litter weight at 21 d; LWW = Litter weight at weaning; PLM = Pre-weaning litter mortality.

[b] Milk yield at lactation intervals of 0–7 d (MY07); 0–21 d (MY021); and 0–28 d (TMY); MCR021 = Milk conversion ratio as g of litter gain per g of milk suckled during 21 d of lactation.

[c] Percentage of the difference refers to the average of the values for V line and Saudi Gabali breed.

* $P<0.05$.

additive effects were non-significant for all the traits. This means that the differences noted earlier between lines V and S are attributable mainly to direct additive effects. These results showed that the genes of line V had better direct additive effects for LSB, LSW, LWB, PLM and MCR021 associated with worse effects for LW21, LWW and milk yield.

The differences in direct additive effects for all litter and lactation traits studied were considerable, ranging from 12.3% to 31.8% relative to the average of the means of both founder genetic groups (Table 6). In a similar study for crossing line V with Sinai Gabali carried out in Egypt to get F_1 (Iraqi et al., 2007), line V was significantly superior to the Sinai Gabali for litter size and weight at birth, but total milk yield was in favour of the latter line. Similarly, some U.S., European and Arabian studies (e.g. Lukefahr et al., 1983a,b; García et al., 2000a,b; Khalil et al., 2004, 2005; El-Deghady, 2005) reported significant direct additive effects on litter and/ or milk traits. Khalil and Afifi (2000) and El-Deghady (2005) in a crossing experiment between NZW and Gabali rabbits reported that NZW rabbits had higher estimates of direct additive effects than Gabali rabbits for litter size and/or litter weight at birth and weaning ($P<0.01$ or $P<0.001$). The other crossbreeding experiment carried out in Egypt by Abd El-Aziz et al. (2002) indicated that estimates of direct additive effects for milk production were mostly in favour of NZW relative to Gabali rabbits.

Some crossbreeding experiments carried out in Arabian countries reported significant values for maternal additive effect on litter and/or lactation traits (e.g. Khalil et al., 1995; Khalil and Afifi, 2000; Al-Sobayil et al., 2005; El-Deghady, 2005).

3.5. Direct, maternal and grand-maternal heterosis

With the exception of LWB and MCR021, estimates of direct heterosis verified that crossbred does were usually associated with significant and favourable heterotic effects since the estimates ranged from 5.3 to 27.5% for litter traits, and from 7.1 to 10.9% for milk yield traits (Table 7). All significant estimates were favourable from a production point of view. In an study by Iraqi et al., (2007) in Egypt, the estimates of individual heterosis for litter size and weight at birth and weaning, and for total milk yield were non significant but the size of this experiment was smaller than ours. Other crossbreeding experiments carried out in Egypt (e.g. Khalil et al., 1995; Khalil and Afifi, 2000; Abd El-Aziz et al., 2002; El-Deghady, 2005) reported individual heterotic effects for litter size, litter weight, and milk yield. Baselga et al. (2003) in a crossbreeding experiment involving three maternal lines got significant individual heterosis for litter size at birth in two of the three possible simple crosses.

Estimates of maternal heterotic effects were significant for LSB (0.73 young) and LSW (0.72 young, Table 7). Khalil et al. (2004) also reported significant maternal heterotic effects for pre-weaning litter traits.

Like grand-maternal additive effects, no significant estimates for grand-maternal heterosis were found for

Table 7
Estimates of direct, maternal and grand-maternal heterosis and their standard errors (±s.e.) for litter and lactation traits

Doe trait	Direct heterosis		Maternal heterosis		Grand-maternal heterosis	
	Estimate±s.e.	%[c]	Estimate±s.e.	%	Estimate±s.e.	%
Litter traits[a]:						
LSB (young)	0.45±0.18*	5.3	0.73±0.19*	8.6	0.08±0.21	0.9
LSW (young)	0.62±0.22*	9.1	0.72±0.22*	10.6	0.06±0.26	0.9
LWB (g)	16.3±11.0	3.9	4.7±11.2	1.1	−6.7±13.7	−1.6
LW21 (g)	148±54*	9.6	−34±54	−2.2	−21±67	−1.4
LWW (g)	237±114*	8.0	−188±115	−6.3	−169±142	−5.7
PLM (%)	−5.7±1.8*	−27.5	−1.7±1.8	−8.2	−2.0±2.0	−9.7
Milk traits[b]:						
MY07 (g)	96±31*	10.9	22±31	2.6	−28±37	−3.2
MY021 (g)	274±108*	8.9	−7±110	−0.2	56±136	1.8
TMY (g)	276±133*	7.1	−43±135	−1.1	−15±166	−0.4
MCR021 (g/g)	0.008±.012	2.7	0.001±.012	0.4	−0.004±.014	−1.3

[a] LSB = Litter size at birth; LSW = Litter size at weaning; LWB = litter weight at birth; LW21 = Litter weight at 21 d; LWW = Litter weight at weaning; PLM = Pre-weaning litter mortality.

[b] Milk yield at lactation intervals of 0–7 d (MY07); 0–21 d (MY021); and 0–28 d (TMY); MCR021 = Milk conversion ratio as g of litter gain per g of milk suckled during 21 d of lactation. $^{*}P<0.05$.

[c] Percentage of the difference refers to the average of the values for V line and Saudi Gabali breed. $^{*}P<0.05$.

any trait (Table 7). These results verify that grand-maternal effects for litter size and litter weight between birth and weaning and milk yield could be of little importance.

4. Conclusions

The use of an exotic line (V line), highly selected for litter size at weaning, and a local breed (Saudi Gabali), well adapted to hot climates, has led to successful creation of two new lines named Saudi 2 and Saudi 3. These lines perform at least as well as the best founder line in a hot climate for litter size and weight at birth and weaning, and for milk yield, so the producers in hot climates could use them.

Line Saudi 2 (3/4V1/4V) was significantly superior to line V for litter size at birth and weaning, litter weight at birth and pre-weaning litter mortality and could be considered as a specialized maternal line in hot climates areas.

The direct additive effects were of considerable importance for all traits associated with significant direct heterosis for the majority, while maternal and grand-maternal effects (additive and heterotic) were mostly non-significant except maternal heterosis for litter size at birth and weaning.

Acknowledgements

This project is supported by a grant (ARP: 18-62) from King Abdulaziz City for Science and Technology in Saudi Arabia.

References

Abd El-Aziz, M.M., Afifi, E.A., Bedier, N.Z., Azamel, A.A., Khalil, M.H., 2002. Genetic evaluation of milk production and litter weight traits in Gabali, New Zealand White rabbits and their crosses in a newly reclaimed area of Egypt. 3rd Scientific Conference on Rabbit Production in Hot Climates, Hurghada, (Egypt), pp. 103–116.

Al-Sobayil, K.A., Al-Homidan, A.H., Khalil, M.H., Mehaia, M.A., 2005. Heritabilities and genetics analysis of milk yield and components in crossing project of Saudi rabbits with Spanish V-line. Livest. Res. Rural. Dev. 17 (10), 1–13 Online Journal www.cipav.org.co/Irrd/Irrd17/10/soba17117.htm. 2005.

Ayyat, M.S., Marai, I.F.M., El-Sayiad, G.H.A., 1995. Genetic and non-genetic factors affecting milk production and preweaning litter traits of New Zealand White does under Egyptian conditions. World Rabbit Sci. 3, 119–124.

Baselga, M., 2004. Genetic improvement of meat rabbits. 8th World Rabbit Congr. Puebla, (Mexico). Programmes and diffusion, vol. 1, pp. 1–13.

Baselga, M., García, M.L., Sánchez, J.P., Vicente, J.S., Lavara, R., 2003. Analysis of reproductive traits in crosses among maternal lines of rabbits. Anim. Res. 52, 473–479.

Boldmann, K.G., Kriese, L.A., Van Tassell, C.P., Kachman, S.D., 1995. A manual for use of MTDFREML. A set programs to obtain estimates of variances and covariance [DRAFT]. U.S. Department of Agriculture, Agricultural Research Service, USA.

Brun, J.M., Baselga, M., 2005. Analysis of reproductive performances during the formation of a rabbit synthetic strain. World Rabbit Sci. 13, 239–252.

Capra, G., Blumetto, O., Elizalde, E., 2000. Meat rabbit production in Uruguay. 7th World Rabbit Congr. Valencia, (Spain), vol. B, pp. 51–58.

de Rochambeau, H., Duzert, R., Tudela, F., 1998. Long term selection experiments in rabbit. Estimation of genetic progress on litter size at weaning. 6th World Congr. on Genet. Appl. to Livest. Prod. Armidale, (Australia), vol. 26, pp. 112–115.

Dickerson, G.E., 1973. Inbreeding and heterosis in animal. In Proceedings of Animal Breeding and Genetics Symposium. In honor of Dr Jay Lush. American Society of Animal Science, pp. 54–77.

Dickerson, G.E., 1992. Manual for evaluation of breeds and crosses of domestic animals. Food and Agriculture Organization of the United Nations, Rome, p. 47.

El-Deghady, A.S., 2005. Genetic evaluation for some productive traits in rabbits. Ph.D. Thesis, Faculty of Agriculture, Banha University, Egypt.

El-Raffa, A.M., 2000. Animal model evaluation of V Line Rabbits raised under Egyptian conditions. Egypt Poultry Sci. 20, 1003–1016.

El-Raffa, A.M., Youssef, Y.K., Iraqi, M.M., Khalil, M.H., García, M.L., Baselga, M., 2005. Developing rabbit lines for meat production in Egypt and Saudi Arabia: overview, synthesizing plan, descriptive performance and future prospects. 4th International Conference of Rabbit Production in Hot Climate, Sharm El-Shiekh, (Egypt), pp. 89–99.

Estany, J., Baselga, M., Blasco, A., Camacho, J., 1989. Mixed model methodology for estimation of genetic response to selection in litter size in rabbits. Livest. Prod. Sci. 21, 67–75.

Ferraz, J.B.S., Johnson, R.K., Van Vleck, L.D., 1992. Estimation of genetic trends and genetic parameters for reproductive and growth traits of rabbits raised in subtropics with animal model. J. Appl. Rabbit Res. 15, 131–142.

García, M.L., Baselga, M., 2002. Estimation of genetic response to selection in litter size of rabbits using a cryopreserved control population. Livest. Prod. Sci. 74, 45–53.

García, M.L., Blumetto, O., Capra, G., Vicente, J.S., Baselga, M., 2000a. Vitrified embryo of two selected Spanish rabbit lines to Uruguay. World Rabbit Sci. 8 (Supp. 1), 139–142.

García, M.L., Baselga, M., Lavara, R., Lavara, F., Vicente, J.S., 2000b. Reproductive characters in crossbreeding among three maternal lines of rabbits. 7th World Rabbit Congr. Valencia, (Spain), vol. A, pp. 397–402.

Garreau, H., Piles, M., Larzul, C., Baselga, M., de Rochambeau, H., 2004. Selection of maternal lines: last results and prospects. 8th World Rabbit Congr. Puebla, (Mexico), vol. 1, pp. 14–25.

Gómez, E.A., Rafel, O., Ramon, J., Baselga, M., 1996. A genetic study of a line selected on litter size at weaning. 6th World Rabbit Cong. Toulouse, (France), vol. 2, pp. 289–292.

Groenoveld, E., 1990. PEST user's manual, Institute of Animal Husbandry and Animal Behaviour. FAL, Germany.

Iraqi, M.M., Shenana, M.E., Baselga, M., 2007. Some factors affecting productive and milk composition characters in a crossbreeding experiment involving Gabali and V-line rabbits in Egypt. World Rabbit Sci. 15 (3), 151–159.

Khalil, M.H., 1994. Lactational performance of Giza White rabbits and its relation with pre-weaning litter traits. Anim. Prod. 59, 141–145.

Khalil, M.H., Afifi, E.A., 2000. Heterosis, maternal and direct additive effects for litter performance and post-weaning growth in Gabali rabbits and their F_1 crosses with New Zealand White. 7th World Rabbit Congr. Valencia, (Spain), vol. A, pp. 431–437.

Khalil, M.H., Afifi, E.A., Youssef, Y.M.K., Khadr, A.F., 1995. Heterosis, maternal and direct genetic effects for litter performance and reproductive intervals in rabbit crosses. World Rabbit Sci. 3 (3), 99–105.

Khalil, M.H., Al-Sobayel, K., Hermes, I.H., Al-Homidan, A.H., 2002. Crossbreeding effects for post-weaning growth, rectal and ear temperatures and respiration rates in crossing Saudi Gabali with Spanish V-Line rabbits. 7th World Congr. on Genet. Appl. to Livest. Prod. Montpellier, (France), n°04–12.

Khalil, M.H., Mehaia, M.A., Al-Homidan, A.H., Al-Sobayil, K.A., 2004. Genetic analysis for milk yield and components and milk conversion ratio in crossing of Saudi rabbits with V-line. 8th World Rabbit Cong. Puebla, (Mexico), pp. 82–89.

Khalil, M.H., García, M.L., Al-Dobaib, S.N., AL-Homidan, A.H., Baselga, M., 2005. Genetic evaluation of crossbreeding project involving Saudi and Spanish V-line rabbits to synthesize new maternal lines in Saudi Arabia: I. Pre-weaning litter, lactation traits and feeding parameters. 4th International Conference of Rabbit Production in Hot Climate, Sharm El-Shiekh, (Egypt), pp. 89–99.

Lukefahr, S.D., Hamilton, H.H., 1997. Heritability and repeatability of maternal performance traits in purebred and crossbred does. World Rabbit Sci. 5 (3), 99–105.

Lukefahr, S., Hohenboken, W.D., Cheeke, P.R., Patton, N.M., 1983a. Doe reproduction and pre-weaning litter performance of straightbred and crossbred rabbits. J. Anim. Sci. 57 (5), 1090–1099.

Lukefahr, S., Hohenboken, W.D., Cheeke, P.R., Patton, N.M., 1983b. Characterization of straightbred and crossbred rabbits for milk production and associative traits. J. Anim. Sci. 57 (5), 1100–1107.

Lukefahr, S.D., Cheeke, P.R., Patton, N.M., 1996. Heritability of milk production and 21-day litter weight and litter size in purebred and crossbred rabbits using an animal model. 6th World Rabbit Congr. Toulouse, (France), vol. 2, pp. 319–323.

Moura, A.S.A.M.T., Costa, A.R.C., Polastre, R., 2001. Variance components and response to selection for reproductive, litter and growth traits through a multi-purpose index. World Rabbit Sci. 9, 77–86.

Rastogi, R.K., Lukefahr, S.D., Lauckner, F.B., 2000. Maternal heritability and repeatability for litter traits in rabbits. Livest. Prod. Sci. 67, 123–128.

Sorensen, P., Kjaer, J.B., Brenoe, Sug, U.T., 2001. Estimates of genetic parameters in Danish White rabbits using an animal model. II. Litter traits. World Rabbit Sci. 9 (1), 33–38.

Testik, A., 1996. The situation of rabbit production and production performances of some exotic rabbits in Turkey. 6th World Rabbit Congr. Toulouse, (France), vol. 3, pp. 435–436.

Wolf, J., Distl, O., Grosshan, T., Seeland, G., 1995. Crossbreeding in farm animals. V. Analysis of crossbreeding plans with secondary crossbred generations. J. Anim. Breed. Genet. 112, 81–94.

Yamani, K.A., 1994. Rabbit meat production in Egypt. Cah. Options Méditerr. 8, 57–64.