Maternal direct additive effects and heterosis on the prolificacy features of rabbits at birth

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6 293 records of three diallelic crossings among four rabbit breeds (California, C; Chinchilla, CH; New Zealand, N and Semigiant, S) were used to determine the individual heterosis (hI), maternal (gM) and direct (gI) additive effects on the prolific features at birth: total born (TB), born alive (BA) and viability at birth (VIAB). A mixed generalized linear model was used with the help of macro GLIMMIX from SAS for estimating the average of each genetic group. The model considered, as fixed effects, the genetic group and the experiment as well as the random effect of the parturition order. The estimations were made through the linear contrast among the average obtained for each genetic group, according to the model of Dickerson. Differences among the genetic groups showed the advantages of the pure N for each features. The maternal additive effects were more important for these features than the direct. The litters of N breed benefit in the TB, while for the VIAB the young rabbit benefit with C genes. The maternal effects were favorable for the CH and N breeds, as maternal breeds for these indicators. A significant heterosis was found for the TB and BA between - 4.6 y - 6.5% for F1 CN and CHN crossing. The differences between the evaluated crossbreeding for these features can be attributed to the maternal and direct additive effect, favorable for using the N and C breeds as paternal and the CH and N as maternal breeds.

Key words: *rabbits, genetic parameters, crossing, prolificacy*

The productivity of rabbit-breeding is determined by the rhythm of parturition, the prolificacy and viability of young rabbits (Camps 1976). These characteristics are in the group of features which offer better benefits when they are improved by the crossbreeding (Ponce de León *et al*. 1997).

Crossbreeding produces changes in the behavior of the offspring, in relation to their progenitors. These changes can be evaluated through the genetic components (heterosis, maternal and direct additive effects) of breeds and their crossings, with the enough precision for predicting the expected behavior of several alternatives of breeds and mating systems (Dickerson 1993).

Considering that in Cuba the first and only sireies in this subject were carried out in the seventies by Ponce de León (1977), and that the performance of breeds and their crossings can vary depending on the environment (Rojas and Sprague 1952 and Piles *et al*. 2004), it was necessary, after 30 years, to estimate the genetic parameters of crossbreeding in these features of economical interest from the information coming from three complete diallelic experiments between four rabbit breeds.

Materials and Methods

A total of 6 293 parturition records from three complete diallelic experiments among the rabbit breeds existing in Cuba (California, Chinchilla, New Zealand, and Semigiant), and briefly described by Ponce de León *et al*. (1997), were used to estimate the crossbreeding parameters for the prolificacy features of rabbits at birth. The experiments, one and two, were developed between July, 1968 and November, 1970, with a difference of a year between them and took place in the rabbit unit "8 de Octubre", located in Zaragoza, belonging to the former Rabbit Plan. The third experiment was carried out between May, 2003 and January, 2005 in the rabbit genetic unit "26 de julio" from Empresa de Ganado Menor (EGAME), in Nazareno. Both units belong to San José de las Lajas, Mayabeque province, Cuba.

For the mating from the three experiments, reproducers and sires from the basic racial foundation stock were selected as representative of the racial genofound in the sirey. The pure reproducers chosen had the phenotypical characteristics of the breed. The young female were selected because of their good physical shape, and the multiparous females for having normal parameters of fertility and prolificacy (Riverón *et al*. 2003).

The mating design (table 1) was carried out through the performance of standards of full diallelic crossing (4x4), regarding the stated by Griffing (1956 a, b) for the design of one (diallelic crossings that rehearse the pure mating, F1 crossings and the reciprocal, and the presence of known maternal effects) and with the structure of a completely random design.

Females of each breed were divided into four mating groups. One group was selected for mating with sires from the same breed, and the other three, with sires from the remaining breeds. The groups were distributed randomly within the unit. The reproducers from each racial group mated with a different sire. Therefore, each sire was assigned several females from different breeds. This allowed maximizing the genetic variability.

The different parturitions of each female came from different sires from the same breed. In order to have a representation of parity and mating management, in each experiment the parturitions were assisted by the

Table 1. Design of mating and number of observations used in the diallelic crossing of four breeds

Maternal Breed	Paternal breed				
	California	Chinchilla	N. Zealand	Semigiant	Total
California	1644	92	98	116	1950
Chinchilla	119	420	108	115	762
N. Zealand	91	93	1320	108	1612
Semigiant	123	77	92	1677	1969
Total	1977	682	1618	2016	6293

same staff, so the results would not be affected by this effect.

The mating was natural, 11 d after parturition, and it was carried out at early hours in the morning, once the heating state of the reproducer was verified. The palpation was carried out in order to check the state of pregnancy at 14-15 d after the mating. Nests of wood with beds of shaving were placed in the cages three days before birth. The living animals were count during the parturition as well as the dead ones and both groups were considered as the total litter.

The animals from experiment one and two were fed with *ad libitum* pellet feedstuff, based on cereals with 18% of crude protein and green forage of alfalfa (*Medicago sativa*) and ramie (*Boehmeria nivea*). The animals used in the experiment three were fed with commercial feedstuff as meal (17-18 % of CP), which was combine with wheat bran at the moment of the offering. The food supply represented around 70% of the requirements, according to the category (Lebas *et al*. 1986). Furthermore, grass forages, mainly king grass (*Pennisetum purpureum*), were offered *ad libitum*.

The genetic parameters of crossbreeding were determined by the prolific features at birth: total born (TB), born alive (BA) and viability at birth (VIAB). The Statistical Analysis System (SAS) for Windows version 9.1.3 (2007) was used to carry out the statistical analysis. The three features used for the sirey, due to its characteristics, are discrete variables. This was confirmed thanks to the test of distribution analysis from this package.

A mixed generalized linear model was used with the help of macro GLIMMIX from SAS for estimating the average of each genetic group. The model included, as fixed effects, the genetic group with 16 classes, and the experiment which contained the three diallelic crossings of the sirey, as well as the random effect of the parturition order (five levels). The model was the same for all the features and it only varied in the function of specific bond, in correspondence to the error attributed to each measure:

$Y_{ijkl} = \mu + p_i + \alpha_j + \beta_k + e_{ijkl}$

Where:

$Y_{ijkl} = f(\mu)$ phenotypical value expected from character in sirey according to the function of specific bond;

μ= average or interception;

p_i=random effect of the i-th parturition order (i=1, …, 5);

α_j= fix effect of the j-th genetic group (j=1, …, 16);

β_k= fix effect of the experimented k-th (k=1, 2, 3);

e_{ijkl}= random error associated with the normally distributed observations.

The model of Dickerson (1969) was used to estimate the genetic parameters of crossbreeding: the individual heterosis (hI), maternal (gM) and direct (gI) additive effects in all the measures in sirey. The estimations were performed through the linear contrast among the average obtained for each genetic group. The contrasts were built according to the definitions of each parameter and with the coefficient shown in table 2

The building of linear contrasts, specifically for the additive effect (direct and maternal effects), was carried out in three stages. During the first stage the individual contrasts among each analyzed breeds where defined. The contrasts of the average effect of one breed with regard to the other three were established during the second stage. Finally, the contrasts to test the differences between the effects of each breed were defined.

Table 2. Parameters of the crossbreeding as linear combinations of the average type of crossing

	Crossing (the breed of the sire is the first)			
	A X A	A X B	B X A	B X B
Direct additive effect (gI)	0.5	0.5	-0.5	-0.5
Maternal additive effect (gM)	0	-0.5	0.5	0.0
Individual heterosis (hI)	-0.5	0.5	0.5	-0.5

$g^I_B = -g^I_A$; $g^M_B = -g^M_A$

Results and Discussion

Differences ($P < 0.001$) were found among the genetic groups for all the sireied measures, where the N breed had the highest average with regard to the CHN and NC crossings for the NT and NV, respectively. For the VIAB, the N and C breeds were different from the S breed, which had the lowest value (table 3).

Table 3. Effects of the genetic group on the prolificacy features at birth

Genetic Group	TB, Nº		BA, Nº		VIAB, %	
	Average	SE ±	Average	SE ±	Average	SE ±
C	1.88^{bd} (6.58)	0.01	1.75^{bc} (5.76)	0.02	2.25^{a}(90.44)	0.12
CCH	1.93^{abcd}(6.86)	0.03	1.77^{abc}(5.89)	0.04	1.88^{ab}(86.76)	0.29
CN	1.91^{abcd}(6.73)	0.03	1.82^{abc}6.14)	0.04	2.57^{ab}(92.87)	0.31
CS	1.97^{ab}(7.16)	0.03	1.86^{ab} (6.40)	0.04	2.35^{ab}(91.26)	0.26
CHC	1.92^{abcd}(6.79)	0.03	1.78^{abc}(5.93)	0.04	2.09^{ab}(89.02)	0.25
CH	1.94^{acd}(6.97)	0.02	1.80^{abc}(6.04)	0.02	2.04^{ab}(88.49)	0.18
CHN	1.84^{d}(6.29)	0.03	1.72^{abc}(5.56)	0.04	2.19^{ab}(89.98)	0.27
CHS	1.91^{abcd}(6.73)	0.03	1.71^{abc}(5.55)	0.04	1.66^{ab}(84.03)	0.22
NC	1.86^{cd} (6.44)	0.03	1.66^{c} (5.26)	0.04	1.60^{ab}(83.24)	0.25
NCH	1.97^{abcd}(7.17)	0.03	1.79^{abc}(5.96)	0.04	1.73^{ab}(85.00)	0.25
N	1.98^{a} (7.23)	0.01	1.84^{a}(6.28)	0.02	2.08a (88.88)	0.12
NS	1.96^{abcd}(7.07)	0.03	1.82^{abc}(6.17)	0.04	2.10^{ab}(89.10)	0.26
SC	1.88^{cd} (6.55)	0.03	1.75^{abc}(5.73)	0.04	2.12^{ab}(89.26)	0.25
SCH	1.96^{abcd}(7.12)	0.03	1.84^{abc}(6.29)	0.05	2.24^{ab}(90.39)	0.36
SN	1.92^{abcd}(6.84)	0.03	1.80^{abc}(6.05)	0.04	2.21^{ab}(90.09)	0.28
S	1.91^{bcd} (6.78)	0.01	1.74^{bc} (5.71)	0.02	1.62^{b} (83.47)	0.11

^{abcd}Parameters with non coinciding superscript in the same column differ at $P < 0.05$ (Kramer 1956)

( ) retransformed average.

The management conditions during the parturition, lactation and feeding provided to the animals could have influenced on the superiority of the N breed with regard to the crossbred. These circumstances did not allow the expected expression of heterosis as consequence of the different mating. This breed, along with the California, is one of the most internationally extended for the business breeding thanks to its excellent results. Both are the base for most of the selection lines (Cheeke 1986, Ozimba and Lukefahr 1991 and Medellín and Lukefahr 2001).

The superiority of the N breed in these features lends certain advantages to this breed, in order to increase the productive levels of rabbit rearing so the main features that determine the productivity of this kind of rearing, have a good behavior in this breed.

Several authors (Khalil *et al*. 1995, Khalil and Afifi 2000, Jaousi *et al*. 2004, Seleem 2005, Abdel Azeem *et al*. 2007 and Al-Saef *et al*. 2008) coincide when informing the marked importance of the kind of mating or crossing in these preweaning characters. This fact coincides with the results obtained in this sirey, apart from the genetic material and statistical analysis used in each sirey.

The estimators for the characters in sirey are shown in table 4. The maternal additive effects were more important for these features than the direct ones. There was no BA with significant direct additive effects which indicates that the sireied breeds have similar values for this character.

These results are thanks to the importance of the maternal effects (effect of the mother of the litter's guide) in these features, although the effect of the genes of the young rabbits influenced on them (Ponce de León 1988 and Orengo *et al*. 2004).

Considering that the direct effect assesses the value of the genes from a determined breed, the average behavior of the assessed breeds varied according to the feature. The litters of N breed benefit in the TB, with one young rabbit more than the others, while the VIAB was beneficial for the young rabbit with C genes which presented 6.7 % of survival more than the others with N and CH genes. The differences for the additive effect of N breed in these two features are because there is a light tendency to increase the mortality with the size of the litter (Torres *et al*. 1986a and b). This tendency is supported by a correlation of 0.24 between these features, although this relation is not linear (Ponce de León 1988).

The differences among breeds for the maternal additive effects demonstrated the potentialities of CH and N breed as maternal breeds of good behavior for these indicators of prolificacy at birth. The S breed was not different from the others as a mother but its

Table 4. Genetic parameters of crossbreeding for the features of prolificacy at birth in diallelic crossings.

		TB, Nº			BA, Nº			VIAB, %.		
		Estimates		SE±	Estimates		SE±	Estimates		SE±
Direct additive effects	$\bar{g}^{I}_{C}$	-0.02^{b}	(-0.14)	0.04	0.07	(0.38)	0.05	0.99^{a}	(6.74)	0.38
	$\bar{g}^{I}_{C}$	-0.07^{b}	(-0.51)	0.04	-0.06	(-0.36)	0.06	0.13^{ab}	(1.79)	0.44
	$\bar{g}^{I}_{N}$	0.16^{a}	(1.09)	0.04	0.08	(0.49)	0.05	-0.60^{b}	(-2.51)	0.38
	$\bar{g}^{I}_{S}$	-0.06^{b}	(-0.44)	0.04	-0.08	(-0.51)	0.05	-0.52^{b}	(-6.02)	0.38
Maternal additive effects	$\bar{g}^{M}_{C}$	-0.07^{b}	(-0.50)	0.03	-0.13^{b}	(-0.76)	0.05	-0.49^{b}	(-4.69)	0.33
	$\bar{g}^{M}_{CH}$	0.10^{a}	(0.68)	0.03	0.09^{a}	(0.15)	0.05	-0.5^{ab}	(-0.44)	0.34
	$\bar{g}^{MN}$	-0.06^{b}	(-0.41)	0.03	0.03^{a}	(0.58)	0.05	0.77^{a}	(7.81)	0.33
	$\bar{g}^{MS}$	0.03^{ab}	(0.23)	0.03	0.00^{ab}	(0.03)	0.05	-0.23^{ab}	(-2.68)	0.34
Individual heterosis	h^{I}_{CCH}	0.01	(0.05)	0.02	0.00	(0.01)	0.03	-0.16	(-1.58)	0.22
	h^{I}_{CCH} (%)		0.74			0.17			-1.77	
	h^{I}_{CN}	-0.05*	(-0.32)	0.02	-0.06	(-0.32)	0.03	-0.08	(-1.60)	0.23
	h^{I}_{CN} (%)		-4.63			-5.32			-1.79	
	h^{I}_{CS}	0.03	(0.18)	0.02	0.05	(0.33)	0.03	0.30	(3.30)	0.21
	h^{I}_{CS} (%)		2.70			5.75			3.80	
	h^{I}_{CHN}	-0.06*	(-0.37)	0.02	-0.07*	(-0.40)	0.03	-0.09	(-1.20)	0.22
	h^{I}_{CHN} (%)		-5.21			-6.49			-1.35	
	h^{I}_{CHS}	0.01	(0.05)	0.02	0.01	(0.04)	0.03	0.12	(1.23)	0.24
	h^{I}_{CHS} (%)	0.73			0.68			1.43		
	h^{I}_{NS}	-0.01	(-0.05)	0.02	0.02	(0.16)	0.03	0.31	(3.42)	0.22
			-0.71			2.69			3.97	

abc Parameters with non coinciding superscript in the same column differ at $P < 0.05$ (Kramer 1956)
( ) retransformed estimators.

contribution was unfavorable for all the features. The presence of this effect for the BA indicates that this is the only genetic cause of variation that determines the behavior of this feature.

The expected negative correlation between the maternal and direct additive effects was evident in these results (Blasco *et al*. 1982 and Garreau and Rochambeau 2003). This aspect has to be considered in the design of a proper policy for the use of breeds.

There are few sireies that inform significant additive effects, maybe because of the similarities in the lines or breeds used. Khalil (1999) also found significant maternal and direct effects for the TB. García-Tomás *et al*. (2006), with lower magnitudes than the used in this sirey, found no differences between the C and R for any of the additive effects in the BA, because this lines presented similar values that prevented to find among them.

With regard to other researches in which the crossing parameters are estimated, the ranges or values of this sirey are very variable. They are more similar to the determined by Khalil (1999), Al Saef *et al*. (2008) and Youssef *et al*. (2008) in similar climatic conditions, where material lines with more than 30 years of selection for prolificacy characters were not used, like in the reports of Brun *et al*. (1992), Baselga *et al*. (2003), Orengo *et al*. (2004), Brun and Baselga (2004 and 2005) and García-Tomás *et al*. (2006). These differences could be also determined by environmental factors, affecting the effect of a line or breed, due to the possible existence of an interaction between the breed and the environment (Rojas and Sprague 1952 and Piles *et al*. 2004).

Besides, the differences among the results could have been determined by the size of the sample and the model used to obtain the contrasting average in each sirey because the majority of these authors used a mixed generalized linear model where they assumed the normal distribution of variables. The present model was linear, generalized and mixed to the distribution of each variable. The genetic material evaluated in each case and the process to improve the populations could have influenced. Breeds used in this sirey settled in Cuba almost 40 years ago. They have received only one import from Canada and their genetic improvement has not been long and constant due to the outbreaks of the Rabbit Viral Hemorrhagic Disease (RVHD) that has provoked the disappearance of genetic herds (Ponce de León 2010).

There were few differences ($P < 0.05$) for the heterosis, which were present in only three of the 18 analysis, specifically for the alive and total born (table 4). These differences were negative, with measures between 4.6 and 6.5%, which reflects the superiority of the pure progenitors from California, Chinchilla and New Zealand species over the F1 CN and CHN crossbreeding.

The presence of heterosis in favor of the California, Chinchilla and New Zealand progenitors allow to highlight the hypothesis of the strictly additive genic action (direct and maternal), found in these same species, according to Falconer (1977).

As Falconer and Mackay (1996) suggested, there are no records of differences in the genic frequency of the two populations that could have caused the non existence of heterosis for the viability at birth.

Heterosis estimations, previously performed with the same breeds in Cuba, showed similar results to those registered in this sirey. Ponce de León (1977) and Ponce de León and Menchaca (1985) also found significant heterosis, but negative for the TB and BA of the CCH crossing. The inferiority of the CN and NC crossings regarding the average of the pure was significant for the TB. The same happened in this sirey despite applying the commercial crossings most used around the world, and that the majority of these improvement programs use these breeds as a maternal way to obtain terminal females and use the advantages of heterosis for the reproductive features (Santacreu 2002 and Roca 2008).

These results does not coincide to those informed by García *et al*. (2010), in spite of using the same breeds and part of the population included in this analysis. These authors found significant heterosis for the TB and BA of the CCH-CHC crossings, with values over 5%. García *et al*. (2012) did not found significant heterosis for the features of prolificacy (TB and BA), whose values were lower than the ones of this sirey. Several authors (Brun and Saleil 1994, Brun *et al*. 1998, Khalil 1999, Orengo *et al*. 2004; Brun and Baselga 2004 and 2005, Al Saef *et al*. 2008, Szendrô *et al*. 2008 and Youssef *et al*. 2008) reported positive and significant heterosis with higher figures for the TB and BA, which differs from the results obtained in this sirey.

Only the heterosis of the CCH, CS and CHS for the TB is within the range from 0 to 6.28 % stated by Abdel-Azeem et al. (2007) for crossbreeding between Baladi Red and other three exotic breeds under the conditions of Egypt, using data obtained through a general linear model (GLM).

In Saudi Arabia, Iraqi *et al*. (2007) determined the resulting heterosis for the crossings between Gabali and V-line from Spain, using average derived from a mixed generalized linear model. These authors did not found a heterosis different from 0 for these features, although the crossing surpassed the pure progenitors with 0.40 young rabbits born alive. In this research, only the CS crossing showed a value of heterosis for this feature, almost close to the results registered by the previous authors, because the remaining five crossings had inferior magnitudes.

The previous results show differences among the evaluated crossings for the features of prolificacy at birth. These differences can be attributed, mainly, to the maternal and direct additive effect, because the values of heterosis were very low for most of the crossings. The additive effects found in this sirey point the N and C as paternal breeds and the CH and N as maternal breeds.

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