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Original article

Evidence for heterosis and maternal effects on rabbit semen characteristics

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Abstract — The analysis concerned 546 ejaculates from 65 bucks from two strains ('1601', a duplicate of the 'Verde' strain from INIA-Valencia, Spain- and '2066' from INRA, France) and their two reciprocal crosses, recorded during a 210 day period spanning from August 1996 to February 1997. Two ejaculates were collected from each buck every three weeks and semen traits were recorded every six weeks when the semen was used for insemination. All semen traits were recorded for both ejaculates except concentration, which was recorded only for the ejaculate selected for insemination (the better of the two ejaculates for mass motility). On average, mass motility (scale of Petitjean, 1965 [24]) was 6.75 (standard deviation 1.01), pH 7.28 (0.33), volume 0.62 mL (0.19 mL), percent of motile spermatozoa (PMS) 70.1% (7.5%), concentration 492×10^6 spz·mL^{-1} (142×10^6), the total number of spermatozoa per ejaculate (TSE) 321×10^6 (110×10^6) and the number of motile sperms per ejaculate (MSE) 231×10^6 (83×10^6). Both strains had similar performances except for the volume of the ejaculate (1601: 0.67 ± 0.04 mL; 2066: 0.52 ± 0.04 mL) and PMS (1601: 69.8 ± 1.4%; 2066: 66.4 ± 1.4%). There was a significant heterosis effect for concentration (37.5% of the parental average), mass motility (6.8%) and PMS (4.1%). Heterosis for the synthetic criteria TSE and MSE amounted to 37.6% and 42.3%, respectively. Strain differences in maternal effects were evidenced: strain 1601 exhibited favourable maternal effects on volume, PMS and mass motility.

rabbit / semen / heterosis / maternal effects

Résumé — **Hétérosis et effets maternels sur les caractéristiques de la semence de lapin.** L'analyse concerne 546 éjaculats issus de 65 mâles de deux souches ('1601', issue par duplication de la souche 'Verde' de l'INIA-Valencia, Espagne- et '2066' de l'INRA, France) et de leurs deux croisements réciproques, contrôlés pendant 210 jours entre août 1996 et février 1997. Les mâles sont prélevés toutes les 3 semaines (2 éjaculats), mais les caractéristiques de la semence sont mesurées toutes les 6 semaines, lors de l'insémination. Tous les caractères sont contrôlés sur les 2 éjaculats sauf la concentration, mesurée uniquement sur l'éjaculat sélectionné pour l'insémination (le meilleur des 2 sur la motilité

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massale). En moyenne, la motilité massale (échelle de Petitjean, 1965 [24]) est de 6,75 (écart-type de 1,01), le pH de 7,28 (0,33), le volume de 0,62 mL (0,19 mL), le pourcentage de spermatozoïdes motiles (PMS) de 70,1 % (7,5 %), la concentration 492×10^6 spz·mL^{-1} (142×10^6), le nombre total de spermatozoïdes par éjaculat (TSE) de 321×10^6 (110×10^6) et le nombre de spermatozoïdes motiles par éjaculat (MSE) de 231×10^6 (83×10^6). Les deux souches ont des performances identiques sauf pour le volume de l'éjaculat (1601 : 0,67 ± 0,04 mL ; 2066 : 0,52 ± 0,04 mL) et PMS (1601 : 69,8 ± 1,4 % ; 2066 : 66,4 ± 1,4 %). On observe un effet d'hétérosis significatif sur la concentration (37,5 % de la moyenne parentale), la motilité massale (6,8 %) et PMS (4,1 %). L'hétérosis sur les caractères synthétiques TSE et MSE s'élève à 37,6 % et 42,3 %, respectivement. La souche 1601 exerce des effets maternels favorables sur le volume, PMS et la motilité massale.

lapin / semence / hétérosis / effets maternels

1. INTRODUCTION

In rabbits, the use of artificial insemination along with a cycled production system [16] is a common practice in meat production. Inseminations are generally performed with cooled semen provided by a semen production farm. In general, semen from different males are pooled before insemination. Numerous works, reviewed by Alvariño [2], have been devoted to factors affecting reproductive performances of male rabbits including the characteristics of semen. Concerning genetic factors, several authors [1, 3, 6, 14, 29] have reported breed comparisons which sometimes include crossbred animals, but the average performance of crossbred males relative to that of males of both pure breeds (i.e. heterosis) has never been estimated. The magnitude of heterosis on semen traits might lead to use crossbred bucks in the semen production farms. The effect of crossbreeding on semen quality traits is not much documented in domestic animal species, except in pig. In his review, Buchanan [10] concluded that crossbred boars generally exhibited larger ejaculate volume, had better semen quality but results concerning sperm concentration varied depending on the study. In cattle, the review concerning the crossbred sire by Thrift and Aaron [28] yielded only one result for heterosis on semen traits, showing heterosis for concentration. Kroetz et al. [20] also evidenced heterosis effects on mass motility, vigour and semen concentration. The aim of the present study was to estimate heterosis, and also maternal effects, on semen characteristics of rabbits within a factorial crossbreeding design including two pure strains and their two reciprocal crosses.

2. MATERIALS AND METHODS

The experiment was performed between August 1996 and February 1997 at the experimental farm for rabbits at the Animal Breeding Department at INRA in Toulouse. Semen quality traits were recorded at three week intervals for a series of 11 insemination series.

2.1. Genetic types

Four genetic types of bucks were studied, two strains and their two reciprocal crosses, with 10 to 13 bucks per genetic type. The strains used were the INRA1601 strain (called A) which descended from the 'Verde' strain of the University of Valencia (Spain) and the INRA2066 strain (called B). The 'Verde' strain has been selected for litter size at weaning since 1983 [15] and strain B for litter size at birth since 1976 [25]. The B strain is used in the French National Scheme of Rabbit Breeding as the

sire strain to make the crossbred parental female (INRA67), used as the dam of meat rabbits. The first generation crosses between the two strains were BA (male B × female A) and AB, the reciprocal cross. These crosses were used to initiate the formation of a synthetic strain [9].

2.2. Semen collection

At the age of about 20 weeks and for two weeks, males were put in the presence of teaser females once a week. During the following month, their semen was collected once a week. Thereafter they entered the reproduction stage and their semen was then collected every three weeks. Since there were two batches of reproduction, each buck was used for insemination only every six weeks. On the day of insemination, the semen from the bucks was collected twice, at 15 minutes intervals. Semen with urine, or with a volume lower than 0.4 mL or a mass motility lower than 6 on the scale of Petitjean [24] was discarded for insemination. The ejaculate with the best mass motility was used for insemination. Between two consecutive services, the bucks went through one semen collection without any semen characterisation. The number of characterised ejaculates per bucks varied between 1 and 12 and averaged 8.

2.3. Traits recorded

At each semen collection attempt, a response was recorded: no collection, collection not fit for insemination (the causes of semen discarding were recorded), or efficient collection (that is fit for insemination). Immediately after the collection, mass motility, pH, volume and percentage of motile sperms (PMS) were estimated according to the methods described by Boussit [8]. Mass motility was recorded according to Petitjean [24] on a scale varying from 0 to 9. Values from 0 to 4 were rare and were therefore pooled at 4 for subsequent analyses. Concentration was estimated using a Thomas-Zeiss cell counter (final dilution 1:200). It was only recorded in the ejaculates used for insemination which represented a selected sample of all ejaculates. From the previous elementary traits, two synthetic criteria were calculated: the total number of spermatozoa per ejaculate (TSE), calculated as the product of volume times concentration and the number of motile sperm per ejaculate (MSE), calculated as the product of TSE times PMS.

2.4. Statistical analyses

The 'total collection rate' (ratio of the collection number to the solicitation number) and the rate of efficient collections (ratio of the efficient collection number to the number of solicitations) were analysed by a Chi-square test. Semen characteristics were analysed on the sample of collections without urine (407 ejaculates), including low volume and low mass motility ejaculates which were discarded from insemination. Data from bucks with less than 4 ejaculates were also discarded. They were analysed using a mixed linear model with the MIXED procedure of SAS [26]. The model included the fixed effects of the genetic type of the male (four levels), the insemination batch and the rank of the ejaculate (No. 1 or 2) and the random effect of the male, allowing for difference in its variance according to the rank of the ejaculate. The interaction between genetic type and insemination batch, previously tested as not significant, was not included in the model. Five insemination batches were defined by regrouping the 11 initial insemination series as follows: 1+2, 3+4, 5+6, 7+8, 9 to 11, so that one batch comprised the majority of bucks of any genotype, in fact between 9 and 12 bucks from any genotype. Direct heterosis was estimated as the difference between the average of crossbred and purebred males and expressed as a percent of the parental average. According to the genetic

model of Dickerson [13], strain differences in maternal effects were estimated as the difference between the two reciprocal crosses AB and BA.

Repeatability of sperm traits for each rank of ejaculates was estimated by the MIXED procedure mentioned before. The VARCOMP procedure was used to estimate the repeatability of the average of the two ejaculates. Correlations between the first and second rank ejaculates were estimated by the COR procedure. Phenotypic correlations between sperm traits were computed as residual correlations from a GLM analysis.

3. RESULTS

3.1. Ability of semen collection for insemination

The genetic type of males did not influence the total collection rate (Fig. 1) but influenced the efficient collection rate: BA males performed better than the three other types (66.9 vs. 43.5% on average for the three types). The main causes of semen elimination were an insufficient volume and the presence of urine (Tab. I). However, it varied according to genetic type: the presence of urine in the semen from A males and an insufficient semen volume from the crossbred males. The B males cumulated both causes.

3.2. Phenotypic correlations between sperm traits (Tab. II)

Among elementary sperm quality traits, the highest correlation was between mass motility and concentration (0.46). Mass motility was positively correlated with PMS but concentration was not. There was an opposition between pH on the one hand and concentration ($r = -0.30$), mass motility ($r = -0.16$) and PMS ($r = -0.13$) on the other hand. The volume of the ejaculate was not correlated with any other elementary trait. But the synthetic criteria TSE and MSE, highly correlated with each other, were positively correlated with mass motility and concentration and negatively with pH.

3.3. Repeatability of sperm traits and correlation between 1st and 2nd rank ejaculates (Tab. III)

Repeatability (r^2) that is the correlation between performances of the same buck in different series was calculated on the sample

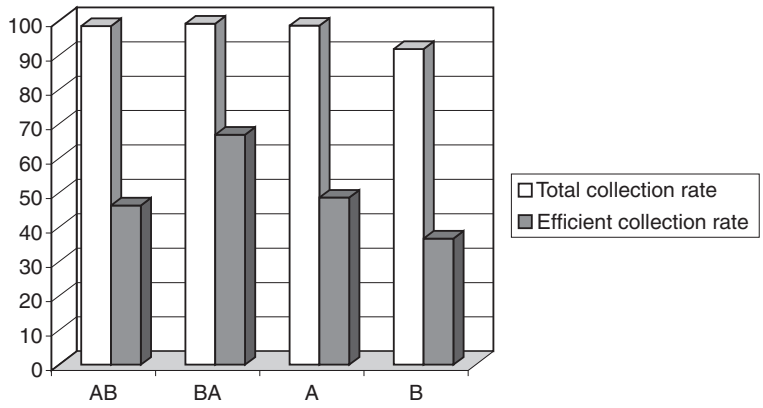

Figure 1. Rates of semen collection according to the genetic type of bucks (sire strain given first).

Table I. Ability of semen collections for insemination: frequency of ejaculate discarding causes according to the genetic type of the bucks.

Genetic type	AB[1]	BA[1]	A	B	Total
Nb ejaculates collected	134	129	138	145	546
Number discarded	71	43	70	87	271
Cause of discarding					
Presence of urine (%)	29.6	34.9	61.4	42.5	42.8
Volume < 0.4 mL (%)	59.2	51.2	20.0	51.7	45.4
Mass motility < 6 (%)	16.9	18.6	27.1	14.9	19.2

[1] Sire strain is given first, A: INRA1601 strain, B: INRA2066 strain.

Table II. Phenotypic correlations between sperm characteristics.

	pH	Volume	PMS	Concentration	TSE	MSE
Mass motility	–0.16*	0.10	0.21*	0.46*	0.45*	0.49*
pH		–0.10	–0.13*	–0.30*	–0.29*	–0.30*
Volume			–0.07	–0.00	0.44*	0.42*
PMS				0.10	0.01	0.13
Concentration					0.85*	0.86*
TSE						0.99*

PMS: percent of motile spermatozoa; TSE: total number of spermatozoa per ejaculate; MSE: number of live spermatozoa per ejaculate.
*: Significantly different from zero ($P < 0.05$).

of the first rank ejaculates, in the second rank ejaculates and also on the average value of both ejaculates. Concerning the first or second rank ejaculates, r^2 ranged from 0.19 to 0.43. Volume was the most repeatable trait for the average of both ejaculates ($r^2 = 0.63$). Average pH was also highly repeatable ($r^2 = 0.57$). PMS and mass motility were less repeatable ($r^2 = 0.47$ and 0.41, respectively). Except for PMS, the correlations between the characteristics of the two ejaculates within one day were generally much lower than those between two ejaculates from different series.

3.4. Analysis of variation of semen quality traits (Tab. IV)

Genetic type influenced mass motility. BA males displayed the highest value. On average, semen of crossbred males had higher motility than semen of purebred males, corresponding to a 6.8% heterosis effect. The significant difference between reciprocal crosses indicated the presence of maternal effects on mass motility, with favourable effects of strain A as compared to strain B. The genetic type did not influence pH. The volume of ejaculates and

Table III. Repeatability of semen characteristics (by rank of ejaculates and on average over both) and correlation between rank 1 and rank 2 ejaculates.

	Repeatability		Average of the two ejaculates	Correlation between ejaculate No. 1 and 2
	Ejaculate No. 1	Ejaculate No. 2		
Mass motility	0.42 ±0.08	0.19 ±0.08	0.41 ±0.09	0.26**
pH	0.26 ±0.04	0.44 ±0.10	0.57 ±0.19	0.11
Volume	0.43 ±0.08	0.43 ±0.08	0.63 ±0.08	0.20*
PMS	0.34 ±0.10	0.34 ±0.10	0.47 ±0.12	0.33**
Concentration	ne	0.75 ±0.05	ne	ne
TSE	ne	0.75 ±0.05	ne	ne
MSE	ne	0.75 ±0.05	ne	ne

PMS: percent of motile spermatozoa, TSE: total number of spermatozoa per ejaculate; MSE: number of motile spermatozoa per ejaculate.
ne: not estimable: too few data for repeatability; concentration, TSE and MSE were never recorded on both ejaculates.
* (**): significantly different from zero at the level of 5% (1%).

PMS varied significantly according to the genetic type. Again for both traits, strain A showed significant superiority over strain B for maternal effects. Heterosis was significant for PMS but not for the volume of the ejaculates. Although the effect of the genetic type on semen concentration did not appear as statistically significant, crossbred male semen was 37.5% more concentrated than that of purebred males. Concentration was not affected by maternal effects. Like concentration, both synthetic criteria TSE and MSE showed no overall differences between genetic types, no maternal effects, but exhibited a high heterosis effect.

The insemination batch had a significant influence on pH, volume, concentration and both synthetic criteria. Concerning pH, a higher value was observed for the first batch (7.48 vs. 7.25 on average for the three others). There was a trend for an increase in volume, concentration and both synthetic criteria with batch number.

Mass motility and pH were influenced by the rank of the ejaculates within one collection day: the second ejaculate showed higher motility and higher pH than the first one.

4. DISCUSSION

The low ejaculation frequency used in this experiment (three-week intervals between ejaculates) [4] was determined by the main concern of the experiment, which was to evaluate female traits, reproducing in two batches at an interval of 21 days [9]. On the basis of male repeatability of semen quantitative traits according to ejaculation frequency [6], a one day per week collection with 2 ejaculates at 15 min intervals, is recommended for male as well as for breed evaluation.

It must be reminded that concentration was only measured in one of the two ejaculates taken at three-week intervals; the ejaculate was chosen based on mass motility for use towards artificial insemination. Due to the correlation between mass motility and concentration, concentration estimates were biased upwards.

Table IV. Significance and lsmeans (stderr) for the genetic type of bucks, insemination batch and ejaculate rank on semen characteristics.

	N_1[1]	Mass motility	pH[3]	Volume (mL)	PMS (%)	N_2[1]	Concentration $\times 10^6$ spz·mL^{-1}	TSE $\times 10^6$ spz	MSE $\times 10^6$ spz
Means (root MSE)	390	6.75 (1.01)	7.28 (0.33)	0.62 (0.19)	70.1 (7.5)	205	492 (142)	321 (110)	231 (83)
Statistical significance									
Genetic type of bucks (**G**)		**	ns	*	***		ns	ns	+
Insemination batch (**B**)		ns	***	**	ns		**	***	***
Ejaculate rank (**R**)		**	+	ns	ns		ns	ns	ns
G estimates									
AB[2]	101	6.70^{b} (0.2)		0.57^{b} (0.04)	67.5^{bc} (1.3)	53	547 (66)	322 (52)	226 (38)
BA[2]	108	7.23^{a} (0.2)		0.66^{a} (0.04)	74.4^{a} (1.3)	56	561 (68)	402 (53)	294 (39)
A	90	6.57^{b} (0.2)		0.67^{a} (0.04)	69.8^{b} (1.4)	50	422 (71)	286 (56)	205 (41)
B	91	6.48^{b} (0.2)		0.52^{b} (0.04)	66.4^{c} (1.4)	46	385 (69)	240 (55)	161 (41)
Heterosis (%)	390	6.8 ±2.6*	ns	ns	4.1 ±1.9*	205	37.5 ±16.7*	37.6 ±19.1*	42.3 ±20.7*
Maternal effect	209	*	ns	+	***	109	ns	ns	ns
B estimates									
Series 1+2	72		7.48^{a} (0.04)	0.55^{c} (0.03)		35	394^{c} (44)	242^{c} (38)	165^{c} (27)
3+4	72		7.23^{b} (0.05)	0.58^{bc} (0.03)		37	467^{bc} (44)	313^{ab} (38)	225^{ab} (27)
5+6	73		- [3]	0.62^{ab} (0.03)		43	487^{ab} (42)	321^{ab} (37)	231^{ab} (26)
7+8	68		7.24^{b} (0.05)	0.59^{b} (0.03)		36	498^{ab} (44)	306^{bc} (38)	216^{bc} (27)
9 to 11	105		7.27^{b} (0.04)	0.68^{a} (0.03)		54	548^{a} (41)	382^{a} (36)	272^{a} (26)
R estimates									
1	204	6.51^{b} (0.14)	7.25^{b} (0.05)			59			
2	186	6.98^{a} (0.11)	7.36^{a} (0.04)			146			

[1]N_1: total number of ejaculates recorded for the first set of traits; N_2: record number for concentration and subsequent traits, recorded on one ejaculate per buck and series. PMS: percent motile sperms; TSE: total number of spermatozoa per ejaculate; MSE: number of live spermatozoa per ejaculate.[2] Sire strain is given first, A: INRA1601 strain, B: INRA2066 strain; [3] pH was not recorded in the series 5 and 6.
+, *, **, *** significant at the level of 10%, 5%, 1%, 1‰.

Our results agree with previous ones on the low frequency of non-response to buck solicitation in rabbits and also on the high frequency of ejaculates which are polluted by urine [5–7, 18]. In this species, the causes of semen discarding have not been studied extensively; however, Bencheick [6, 7] already found, for the B bucks, a high percentage of ejaculates contaminated by urine (13.4%). He also mentioned a lower volume of the ejaculates of B (INRA2066) bucks, compared to the INRA1077 strain bucks. This observation is in agreement with the high percentage of semen elimination for an insufficient volume in the B strain.

Semen pH was negatively correlated with concentration, mass motility and the percent of motile spermatozoa. Such an opposition between pH and other sperm traits, particularly concentration and mass motility, had been previously found by More O'Ferral and Meachan [22] and Bencheikh [6]. This may be due to the metabolic activity of the spermatozoa, which use fructose as the major source of energy [19] and release lactic acid which decreases pH [11].

Strains A and B showed differences for the volume of the ejaculate and PMS and their crossbreds exhibited heterosis for concentration, TSE, MSE, mass motility and PMS. Of course, strain differences in sperm characteristics had already been evidenced in the literature but the influence of crossbreeding on sperm traits had never been estimated. Bencheick [6] found a general superiority of the INRA1077 strain over the INRA2066 strain for all sperm traits, with twice as many motile sperms per ejaculate in the former strain. Frölich and Venge [17] and Venge and Frölich [29] stated that the differences in volumes between the genetic types studied (Polish – a small body sized breed-, two large sized breeds and one crossbred population) could be accounted for by the mean weight of the bucks but differences in concentration could not be accounted for by this. They found that, in relation to body weight, the number of sperms delivered by crossbred males was 1.1–2 times higher than that delivered by pure breeds and interpreted this phenomenon as an effect of heterosis. Abo El-Ezz et al. [1], comparing imported purebred bucks (Chinchilla and Bouscat) with all the reciprocal crossbreds of these breeds and two local Egyptian strains found no crossbred superiority of volume and concentration over the imported breeds (but average body weight also differed between purebreds and crossbreds). However crossbreds showed a lower percentage of dead and abnormal spermatozoa. Heterosis effects on sperm production may be either due to differences in age at sexual maturity (sperm production of crossbred animals starts and increases earlier than in purebred animals, but adult sperm production is similar) or to differences in adult sperm production. In our study, no interaction between genetic type and age (rank of batch) was evidenced. It can therefore be concluded that heterosis was not due to earlier sexual maturity of crossbred bucks but was expressed all along the lifetime investigated. In pigs, heterosis for sperm concentration is not a general rule but it was found in most experiments involving young boars [10], in relationship with heterosis on sexual precocity.

From the comparison between reciprocal crosses, maternal effects were inferred for volume, mass motility and percent motile spermatozoa: strain A would exert favourable maternal effects on these traits compared to strain B. Maternal effects are indeed only one of the possible explanations for differences between reciprocal crosses; sex-linked or imprinting effects might also explain such differences. An effect of the mitochondria, maternally transmitted cell organites involved in energy metabolism is a particularly appealing hypothesis for traits related to metabolism such as mass motility or percent motile sperm. A difference in pH between the reciprocal

crossbreds, although non significant (AB: 7.30; BA: 7.25), was congruent with the interpretation of a low pH as an indicator of high metabolic activity of semen.

The total number of spermatozoa per ejaculate increased with batch number. The insemination batch effect is a composite effect including age of males, season (from August to February). It is likely that the increase in sperm production was mainly due to age, given that the batches of higher rank occurred in winter, a season known to decrease sperm production [23].

Concerning the influence of the rank of the ejaculate on semen characteristics, the higher mass motility found in the second ejaculate is in agreement with the results of Bencheikh [6] and Theau-Clément et al. [27]. Several authors have found a higher concentration and production of spermatozoa in the second ejaculate [6, 12, 21, 23, 27]. Our study did not allow verification of this since concentration was never recorded on both ejaculates from one buck and moreover it was only recorded on a selected sample of the ejaculates.

5. CONCLUSION

The genetic type of males influenced sperm production on both levels of qualitative and quantitative traits, with a variation between types amounting to 30% for some traits. An heterotic effect of 42.3% was observed on the number of motile spermatozoa per ejaculate. Crossbred superiority was particularly obvious in the BA males which cumulated heterosis and favourable maternal effects of the A dam strain. Maternal influences appeared significant for mass motility, percent of motile spermatozoa and volume. They could be accounted for by maternal transmission of the mitochondria, cell organites involved in energy metabolism. These results, obtained in a very extensive ejaculation frequency, encourage the investigation of heterosis and maternal effects with a frequency more adequate for semen characteristics evaluation. The relationship between sperm characteristics and fertility also remains to be investigated.

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