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animal

Environmental and genetic variation factors of artificial insemination success in French dairy sheep

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*Artificial inseminations (*n *= 678 168) recorded during 5 years in five French artificial insemination (AI) centres (2 'Lacaune', 1 'Manech tête rousse', 1 'Manech tête noire' and 1 'Basco béarnaise') were analysed to determine environmental and genetic factors affecting the insemination results. Analyses within centre-breed were performed using a linear model, which jointly estimates male and female fertility. This model combined four categories of data: the environmental effects related to the female, those related to the male, the non-sex-specific effects and finally the pedigree data of these males and females. After selection, the environmental female effects considered were age, synchronisation (0/1) on the previous year, total number of synchronisations during the female reproductive life, time interval between previous lambing and insemination, already dry or still lactating (0/1) when inseminated, and milk quantity produced during the previous year expressed as quartiles intra herd * year. The environmental male effects were motility and concentration of the semen. The non-sex-specific effects were the inseminator, the interaction herd * year nested within the inseminator, considered as random effects and the interaction year * season considered as a fixed effect. The main variation factors of AI success were relative to non-sex-specific effects and to female effects. Heritability estimates varied from 0.001 to 0.005 for male fertility and from 0.040 to 0.078 for female fertility. Repeatability estimates varied from 0.007 to 0.015 for male fertility and from 0.104 to 0.136 for female fertility. These parameters indicate that genetic improvement of AI results through a classical polygenic selection would be difficult. Moreover, in spite of the large quantity of variation factors fitted by the joint model, a very large residual variance remained unexplained.*

Keywords: dairy sheep, artificial insemination, environmental variation, genetic parameters, fertility

Introduction

The wide development of artificial insemination (AI) in French sheep farming date from the early 1970s. At this time, a hormonal treatment to induce and synchronise the oestrus and ovulation of females became available. Fertility rate after cervical insemination using frozen-thawed semen in sheep is very low (Salamon and Maxwell, 1995) and unacceptable compared to results obtained with fresh semen. Even though intrauterine insemination of frozen-thawed semen by laparoscopy results in acceptable lambings, the cost, the small surgery and the expertise required by this procedure limit its utilisation. For these reasons, more than 99% of the 848 691 French sheep AI realised in 2005 were done with fresh semen collected a few hours before insemination (Perret and Lagriffoul, 2006).

In the Roquefort area, dairy industries collect milk from November to July. In this context, AI associated with hormonal treatment allowed breeders to fit the ewe lambing with the beginning of the milk-collecting period. It also allowed setting up an efficient breeding scheme based on planned mating, progeny testing and dissemination of genetic merit. Presently, about 90% of the ewes in the nucleus are inseminated each year for these genetic purposes, and approximately 300 000 ewes are inseminated out of the nucleus to disseminate the genetic progress (Perret and Lagriffoul, 2006). Other breeding schemes exist for dairy sheep breeds located in the Pyrenean Mountains. They tend more or less towards a similar organisation as the Lacaune scheme although the insemination rate of ewes within the nucleus is lower (about 60%).

In order to improve their efficiency, French AI centres are interested in the identification of the main environmental effects affecting the AI result, and the estimation of the corresponding genetic parameters. This complex trait may be viewed as a combination of two main traits, which can be analysed jointly (David *et al.*, 2007b), one relative to the female (i.e. female fertility), the other relative to the male

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(i.e. semen fecundancy or male fertility). Combining all this information in a joint model should improve the precision of the estimates. The aim of this paper was to analyse the environmental and genetic effects that affect AI success using a joint model. The implementation of a joint model could be made since, in the French sheep situation, each on-farm recorded insemination can be matched to the corresponding ejaculate produced at the AI centre and to the corresponding outcome, which is a binary response observed at lambing of either success (1) or failure (0).

Table 1 *Global percentage of AI success, number of inseminations and animals involved in the study for each breed/centre*

AI centre Breed	CDEO MTN	CDEO BB	CDEO MTR	Lac_1 Lac	Lac_2 Lac
Number of AI	32793	34468	135623	247651	227633
Number of females	17295	18583	74136	123574	117384
Number of males	220	257	963	1433	1517
Animal in pedigree	26185	28967	115627	225680	218566
Global % of AI success	54.6	56.8	57.7	66.7	65.8

AI = artificial insemination; MTN = Manech tête Noire; BB = Basco béarnaise; MTR = Manech tête rousse; Lac = Lacaune.

Material and methods

Data

The present study refers to dairy sheep inseminations performed on private farms from 2001 to 2005 by three AI centres. Centre 1 (Centre Départemental de l'Elevage Ovin, CDEO) is located in the French Basque region and performs inseminations for three breeds: Manech tête rousse (MTR), Manech tête noire (MTN) and Basco-béarnaise (BB). Centres 2 (Lac_1) and 3 (Lac_2) are located in the Roquefort region and both perform inseminations for the Lacaune (Lac) breed. These AI concern adult ewes (more than 1-year old) in flocks that participate in the selection scheme of these four dairy breeds. The numbers of inseminations per centre and breed with the global rate of AI success are shown in Table 1. Data came from a specific database built by the ANIO (Association Nationale des centres d'Insémination Ovine) for this study. This base combined information from two data sources. The first source was the sheep AI centres, which provided information on males (e.g. identification, age), characteristics of semen for a particular collect (e.g. volume, concentration, motility) and identification of ewes inseminated a few hours after collection by the fresh semen of a given sire. The second source originated from the French national performances recording scheme that holds pedigree information and ewe performances (e.g. reproduction type, date of lambing, number of lambs born). For each breed/centre, less than 4% of the initial data set containing missing data was removed from the data samples.

Rams and semen management. Rams belonged to dairy selection schemes and ranged in two categories: young rams ($<$1-year old) under progeny testing and adult rams ($\geqslant$2 years) having proven genetic value. In order to increase their libido, their semen production and their semen quality, these males were given a melatonin implant (Mélovine®; CDEO centre) or a photoperiodic treatment (Lac_1 and Lac_2 centres) according to recommendations, about 2 months before the beginning of the annual collecting period (Chemineau *et al.*, 1989). Ejaculates were obtained after natural ejaculation in an artificial vagina; only those collected during the intensive period of ram collection (May to August) were considered in this analysis. Each ram was collected from 1 to 5 years and within a year the interval between its semen collections varied from 1 to 32 days.

Trait definition and data analysis. For a given ram, the pool of 1 to 3 successive ejaculates, obtained over a 2 to 5 min period, was evaluated immediately after collection. Three traits were evaluated for each pool: volume that was read directly from a graduated collection tube (ml), semen concentration that was determined using a standard spectrophotometer (10^6 spermatozoa/ml) and mass motility that was scored subjectively on a 0 to 5 scale. The ejaculate volume was defined as the pool volume divided by the number of ejaculates. After measuring the quality (volume, concentration and motility assessment), semen with a motility higher than 4 and a concentration higher than 1.4×10^9 spermatozoa/ml was diluted in a milky extender (Baril *et al.*, 1993) to prepare about 10 doses with a concentration of 1.4 or 1.6×10^9 spermatozoa/ml. Each dose was stored at 4°C in a 0.25 ml straw until insemination a few hours later.

Female management and inseminations. In the French dairy sheep system, there is only one reproduction period, which extends from late spring to summer and corresponds to the end of the previous milking period. In each flock, at the beginning of the joining period, breeders with the help of the selection scheme organisation choose the ewes to inseminate. After having received a synchronisation treatment (FGA vaginal sponge (Sanofi or Intervet) inserted for 14 days, followed by a PMSG injection at withdrawal (Folligon® or PMSG; Sanofi Animal Health Ltd, Libourne, France)), these ewes received cervical insemination with fresh semen irrespective of oestrus expression about 55 h after sponge withdrawal according to standard recommendations (Chemineau *et al.*, 1991). They were subsequently systematically joined with males 6 days after insemination to ensure fecundation by natural mating. The interval between insemination and lambing dates was used to determine the fertile oestrus (after insemination or natural mating).

Model

For each insemination, many potential risk factors were recorded and analysed. They were clustered into three categories: the effects related to the female (synchronisation, reproductive and productive career, as well as the female genetic effect), those related to the male (sperm characteristics, collection, as well as the male genetic

Table 2 *List of environmental effects tested in the analysis*

Tested effects	Significant effects retained in the final model
Fixed effects	
Non-sex-specific effects	
Year * fortnight (2001 to 2005; fortnight 10 to 15)	✓
Set of AI within flock – year	
Interval between set of AI (in weeks)	
Interval between end of female treatment and AI	
Number of AI per operator within a set of AI (class of 50)	
Effects linked to male	
Age of male (in years)	
Interval between semen collections (in days)	
Number of ejaculate at each collection	
Collection period (AM – PM)	
Initial semen concentration (by class)	✓
Motility (by class)	✓
Semen dilution	
Interval between semen collection and AI	
Male class (in progeny test, proven, elite for milk production)	
Effects linked to female	
Age of female (in years)	✓
Lactation number	
Age at first lambing (in months)	
PMSG dose	
Post-partum interval (lambing – AI)	✓
Result of the previous AI	
Litter size at the previous lambing	
Class of milk yield (four quartiles within flock * year)	✓
Total number of treatment	✓
Milking status (dry, in lactation, unknown)	✓
Female category (dam for females, dam for sire, other)	
Random effects	
Flock * year (AI operator)	✓
AI operator	✓

AI = artificial insemination.

effect) and non-sex-specific effects that were either related to the insemination (operator, interval collection-AI, etc.) or common to all previous categories (year, fortnight, flock). All environmental effects tested in the analysis are presented in Table 2.

Five separate analyses within breed/centre were performed using the linear model already described by David *et al.* (2007b), which jointly estimates male and female effects by considering the AI success as a continuous variable.

The model was as follows:

$$y = X_c\beta_c + Kc + Lh + X_m\beta_m + Z_m u_m + W_m p_m$$
$$+ X_f\beta_f + Z_f u_f + W_f p_f + \varepsilon$$

where $\boldsymbol{y}$ is the vector of the binary result of insemination, β_f, β_m and β_c are vectors of fixed effects related to the female, the male or common to both sexes, respectively. $\boldsymbol{u}_f$ and $\boldsymbol{u}_m$ are vectors of female and male random genetic effects, respectively. $\boldsymbol{p}_f$ and $\boldsymbol{p}_m$ are vectors of female and male random permanent environmental effects, $\boldsymbol{c}$ and $\boldsymbol{h}$ are the random vectors of AI operator and flock * year intra AI operator effects, respectively. ε is the vector of residuals. $\boldsymbol{X}_f$, $\boldsymbol{X}_m$, $\boldsymbol{X}_c$, $\boldsymbol{Z}_f$, $\boldsymbol{Z}_m$, $\boldsymbol{W}_f$, $\boldsymbol{W}_m$, $\boldsymbol{K}$ and $\boldsymbol{L}$ are the corresponding known incidence matrices. All random effects are distributed as a centred normal distribution with variance covariance matrix equal to $A\sigma_i^2$ for the genetic effects i ($i = u_f$ or u_m), and $I_j\sigma_j^2$ for the other random effects j ($j = c, h, p_f, p_m, \varepsilon$) where $\boldsymbol{A}$ is the known relationship matrix, $\boldsymbol{I}_j$ are identity matrices of appropriate order. Random effects are assumed to be independent of each other. In particular, it supposes that male and female fertility traits are genetically independent, which has been shown by David *et al.* (2007b).

The fixed effects and all one-way interactions with biological meaning included in the model were preliminarily selected step-by-step by comparing the nested models with the likelihood ratio test. For this selection, models were fitted using the mixed procedure of SAS version 8.1 (SAS®, 1999) and the maximum likelihood method. Once the final model was chosen, estimations of fixed effects and variance components were obtained using Asreml software (Gilmour *et al.*, 2002). Heritability was computed as $\sigma^2_{u_m}/\sigma^2_T$ for male fertility and $\sigma^2_{u_f}/\sigma^2_T$ for female fertility; repeatability was computed as $(\sigma^2_{u_m}+\sigma^2_{p_m})/\sigma^2_T$ for male fertility and $(\sigma^2_{u_f}+\sigma^2_{p_f})/\sigma^2_T$ for female fertility with $\sigma^2_T = \sigma^2_{u_m}+\sigma^2_{p_m}+\sigma^2_{u_f}+\sigma^2_{p_f}+\sigma^2_{\varepsilon}$.

Final model

After selection, female effects considered in the final model were age, time interval between previous lambing and insemination, milking status for the female: already dried or still milking when inseminated, milk quantity produced during the previous year expressed as quartile intra flock * year and total number of synchronisation treatments received during the career. Male effects entering this model were semen motility and concentration. Non-sex-specific effects were year * fortnight combination. These significant effects are listed in Table 2. The random effects that were also included in the model along with the male and female genetic effects were the male and female permanent environmental effects as well as the AI operator, and the flock * year interaction nested within the AI operator.

Results

Environmental fixed effects

The main fixed effects that significantly affected the AI success are presented according to their importance. Table 3 shows for each effect and breed/centre, the variation range of the least squares mean and the significance of the effect.

*Year * fortnight interaction*. In all breed/centres, the year * fortnight interaction effect was significant ($P < 0.01$). It was the main effect affecting AI success; however, there was no general trend associated with year. Thus for Lac$_2$, AI success increased slightly from 2001 to 2005 while it decreased for MTN (Figure 1a) and did not present any trend for the other breed/centres. Changes with fortnight were large between years (Figure 1b for MTN) and no clear common trend could be viewed.

Other fixed effects. Least squares solutions of fixed effects affecting AI success for each breed/centre and plotted in standard error unit are given in Figure 2. For multiparous ewes, the *post-partum* duration until insemination (Figure 2a) had a very large effect on AI success in all breed/centres. Under French dairy sheep management, lengthening this interval from about 3 to 7 or 8 months increased AI success by 10% to 20% according to the breed.

Female ages (Figure 2b) were at least highly significant ($P < 0.01$) for all breed/centres. AI success tended to decrease regularly after two years, except for MTR and MTN breeds, for which the maximum success was reached with 3- and 4-year old ewes, respectively.

The regular increase of AI results with increasing semen motility was very clear in all situations (Figure 2c). However,

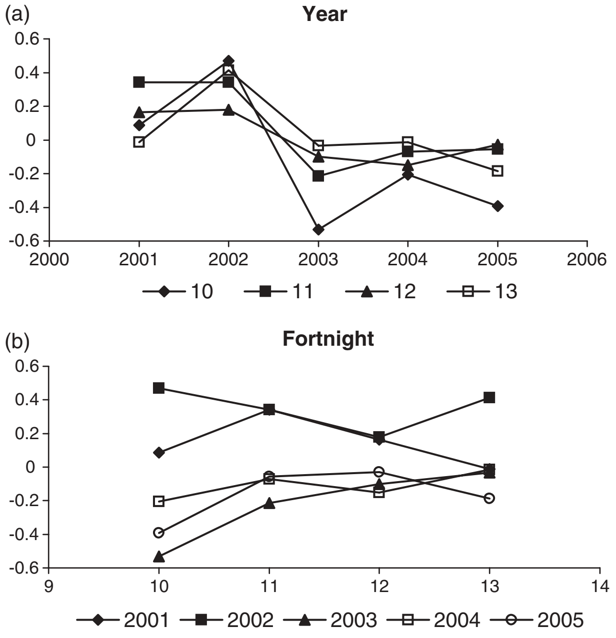

Figure 1 Estimated values of AI success for the year * fortnight interaction in the Manech Tête Noire breed (MTN) in relation to year (a) and fortnight (b) levels.

Table 3 *Variation range of least squares means of the main environmental fixed effects for AI success for each breed/centre and level of significance (in brackets)*

AI centre Breed	CDEO MTN	CDEO BB	CDEO MTR	Lac$_1$ Lac	Lac$_2$ Lac
Year * fortnight	0.20‡ (***)	0.35 (***)	0.19 (***)	0.14 (***)	0.14 (***)
Lambing–AI interval	0.10 (***)	0.13 (***)	0.13 (***)	0.20 (***)	0.14 (***)
Female age	0.11 (***)	0.07 (***)	0.07 (***)	0.12 (***)	0.13 (***)
Sperm motility	0.06 (***)	0.10 (***)	0.09 (***)	0.07 (***)	0.035 (***)
Total synchronisation per female	0.09 (***)	/	0.05 (**)	0.06 (***)	0.032 (*)
Milk production quartile	0.03 (**)	0.03 (*)	0.044 (***)	0.035 (***)	0.035 (***)
Semen concentration	0.03 (*)	0.035 (***)	/	0.01 (***)	/
Milking status	0.03 (*)	/	/	/	/

AI = artificial insemination; MTN = Manech tête Noire; BB = Basco béarnaise; MTR = Manech tête rousse; Lac = Lacaune.
‡0.20 → difference between lowest and highest fertility due to this effect (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

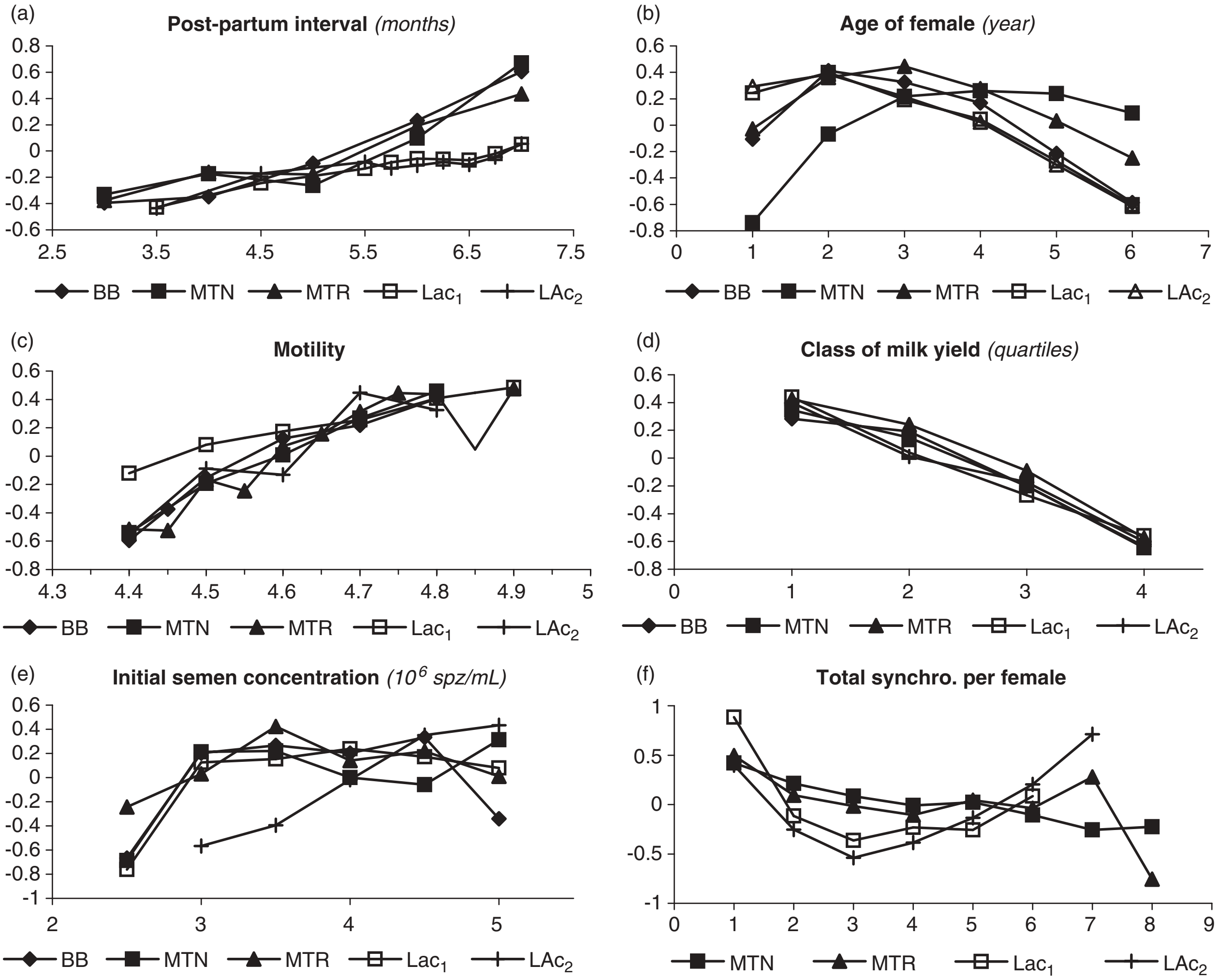

Figure 2 Least square means of AI success in proportion to maxima variability within breed/centre for: (a) *post-partum* interval until AI for multiparous ewes, (b) female age, (c) semen motility, (d) quartile of milk production, (e) semen concentration and (f) total number of synchronisation treatments per female.

this significant effect ($P < 0.05$) accounted only for 3.5% to 10% of the success rate according to the breed/centre. The quartile of total milk yield evaluated each year within flock at the end of the lactation of a ewe had a significant ($P < 0.05$) effect on the success of the following insemination (Figure 2d); however, this effect was low since the difference between extreme quartiles was about 3.5% of success.

The total number of synchronisation treatments that females had received during their life had a curvilinear effect on the AI results (Figure 2f). For a low number of treatments, the results highly decreased at each new treatment, while success difference between successive AI was almost nil or slightly positive at an older age. The highest difference (from 3% to 6%) was observed between ewes that had received 1 and 2 treatments.

Concentration of semen before processing affected the AI results in all breed/centres except one. We observed a fertility gap (about 3%) on three occasions when using semen with a concentration lower and higher than 2.5×10^6 spermatozoa/ml. The other breed/centres presented a similar increase of the AI results with increasing semen concentration. Although for this breed/centre we observed a threshold concentration effect, it was higher (around 4×10^6 spermatozoa/ml) and not so drastic (Figure 2e).

Although the very same trend was observed for all breed/centres, the effect of milking status of a ewe was significant for only two breeds (MTN and MTR). The negative consequence of inseminating still milking ewes was low and induced a loss of about 3% of success compared to AI on already dried ewes.

Random effects and genetic parameters

Estimations of all variance components (Table 4) were very consistent among breed/centres; moreover, they were all very low regarding the residual variance that represented between 81% and 84% of the total phenotypic variance. The largest variance components were those of the permanent female effect that accounted for about 40% of the explained variance. Variances of the female additive genetic effect were of the same order, so the sum of these two

Table 4 *Variance components and genetic parameter estimates for each breed/centre, standard error of estimate in brackets*

	AI centre	CDEO	CDEO	CDEO	Lac_1	Lac_2
Variance components	Breed	MTN	BB	MTR	Lac	Lac
Flock * year (IA Op.)		0.0065	0.0068	0.0079	0.0043	0.0046
IA operator		0.0007	0.0004	0.0006	0.0008	0.0002
Additive male	$\sigma^2_{u_m}$	0.0004	0.0009	0.0006	0.0005	0.0002
Additive female	$\sigma^2_{u_f}$	0.0093	0.0178	0.0123	0.0109	0.0112
Permanent male	$\sigma^2_{p_m}$	0.0028	0.0015	0.0011	0.0017	0.0019
Permanent female	$\sigma^2_{p_f}$	0.0149	0.0132	0.0151	0.0157	0.0137
Residual	σ^2_{ε}	0.2076	0.1985	0.2019	0.1852	0.1893
Total	σ^2_T	0.2350	0.2319	0.2310	0.2140	0.2163
Repeatability of AI success						
For males	$(\sigma^2_{u_m} + \sigma^2_{p_m})/\sigma^2_T$	0.014 (0.002)	0.010 (0.002)	0.007 (0.001)	0.010 (0.001)	0.010 (0.001)
For females	$(\sigma^2_{u_f} + \sigma^2_{p_f})/\sigma^2_T$	0.103 (0.008)	0.133 (0.008)	0.119 (0.004)	0.124 (0.003)	0.115 (0.003)
Heritability of AI success						
For male component	$\sigma^2_{u_m}/\sigma^2_T$	0.002 (0.003)	0.004 (0.002)	0.003 (0.001)	0.002 (0.001)	0.001 (0.001)
For female component	$\sigma^2_{u_f}/\sigma^2_T$	0.039 (0.007)	0.077 (0.009)	0.053 (0.004)	0.051 (0.003)	0.052 (0.003)

AI = artificial insemination; MTN = Manech tête Noire; BB = Basco béarnaise; MTR = Manech tête rousse; Lac = Lacaune.

female components accounted for about 75% of the variance part explained by the model and about 11% of the total variance. In contrast, the two male variance components were extremely low for all breed/centres. Heritability of female success was always low, varying from 0.04 to 0.08 but different from zero; the repeatability was about 0.10. Genetic parameters were consistently much lower for the male component of AI success. Thus, repeatability of the male component was about 1% and heritability was in some occasions not different from zero.

The variance due to the flock * year interaction within the AI operator accounted for about 3% of the total variance, while the component for the AI operator explained only 0.2% of the total variance.

Discussion

This study considered the binary results of artificial insemination as a continuous variable and we used linear models that are more suitable for continuous than for categorical data. Nevertheless, several studies showed that linear models and threshold models give similar results in some conditions on the incidence of the categorical trait (Meijering and Gianola, 1985; Boichard and Manfredi, 1994), and the sire family size (Ramirez-Valverde *et al.*, 2001). These conditions were respected in our data set. Moreover, a comparison of both methods using data of one breed/centre analysed in the present study has already been presented by David *et al.* (2007b); the differences between these methodologies were negligible. The model was mainly built to estimate genetic parameters of AI success free of environmental variation effects; therefore, some effects strongly linked to genetic effects were not included in this model. For instance, AI success was not adjusted for the result of the previous insemination although we had shown in preliminary studies that it was one of the major variation factors. For this reason, breeders should avoid inseminating females that were not pregnant at the previous AI.

The results of independent analysis made on the five breed/centres were strongly consistent and agreed very well with the literature in spite of the breed diversity, the variability of male management in the three AI centres and the different environmental conditions in which females are bred. In our study, each AI centre uses a specific photoperiodic treatment for stimulating testicular development and optimising sperm production to fit their specific seasonal demand (Briois *et al.*, 1988; Arranz *et al.*, 1995); consequently, there is no global trend of AI success with months. In contrast with observations on dairy cattle (Barbat *et al.*, 2005), there is no clear trend of AI success over this period in French dairy sheep, except for one centre.

The effect of *post-partum* delay on sheep fertility is well known and Cognié *et al.* (1984) recommended not to inseminate ewes with less than 150 *post-partum* days, which is the time interval threshold observed in our study while this admissible delay is 50 days for Anel *et al.* (2005). The decrease in AI success with increasing female age is a very classical effect; our results agree with the 15% drop per year described a long time ago in the Lacaune breed by Colas *et al.* (1973) and recently in a Spanish dairy breed by Anel *et al.* (2005).

In French sheep, dairy production lactation of ewes are seasoned and synchronised. At the end of the lactation period, ewes of a flock that were given the same feeding presented a variability of body condition score, which was related to the total milk quantity they have produced and therefore to their quartile of production within flock and year. The broad relationship between body condition score and fertility viewed in this way was slightly positive (about 3 points of fertility drop between extreme classes of milk production quartile). In dairy cattle, Roche (2007) found a positive effect of the body condition score on the ratio of pregnant cows at first service, and in a more precise study Grimard *et al.* (2006) reported a similar positive effect of the body condition score on late embryonic survival.

We found in our experiment, above the culling threshold, a permanent and positive relationship between motility and fertility. This small effect contrasts with the absence of effect previously found by Colas (1981) in Ile de France and by Duval *et al.* (1995) in one Lacaune centre even if this centre displayed a lower effect in our study. But this agrees with the important role of this characteristic on the transport and survival of spermatozoa in the female reproductive tract and fertility (Salamon and Maxwell, 2000). A positive relationship between the percentage of motile spermatozoa and female fertility is well documented in other species (Linford *et al.*, 1976; Correa *et al.*, 1997; Colenbrander *et al.*, 2003; Gadea, 2005).

The threshold effect of semen concentration on AI results has not been previously noticed. A lack of effect is generally claimed, but it is in studies that involved a low number of data (Hulet *et al.*, 1965; Colas, 1981). This absence of effect was also found in the Lac_2 centre, which is the only breed/centre where the effect was not significant in our study (Duval *et al.*, 1995).

The operator effect, which in our study was considered as a random effect, explained very little of the total variance. However, the theoretical extreme values provided by a Gaussian distribution would result in a large difference: 9 to 16 points, according to the breed/centre. This agreed with results in the literature (Duval *et al.*, 1995; Anel *et al.*, 2005).

The very low male components of additive genetic variance and permanent environmental variance agreed with the general results obtained in other species for fecundancy (Varona and Noguera, 2001; Piles *et al.*, 2005). They also agreed with the low variance components reported for service sires in many studies of female fertility (Weller and Ron, 1992; Averill *et al.*, 2004; Donoghue *et al.*, 2004; Robinson and Buhr, 2005).

Female components of AI success are in the range of values found in the literature for female fertility of sheep as well as other species (Matos *et al.*, 1997; Boichard *et al.*, 1998; Ranberg *et al.*, 2003; David *et al.*, 2007b). Although these components were low compared to the residual variance, they induced a genetic coefficient of variation of 16% to 23% according to breed/centres, which would permit to envisage selection on this trait.

There are very few joint estimations of genetic parameters for female fertility and male fecundancy. The few studies in cattle (Ranberg *et al.*, 2003), rabbits (Piles *et al.*, 2005) or pigs (Varona and Noguera, 2001) did not consider the effect of semen characteristics on mating success. David *et al.* (2007b) compared different models for the genetic analysis of AI success in sheep and considered the environmental effects linked to semen and showed that it was the best model. However, the very large residual variance was poorly affected by the model used and genetic parameters remained nearly constant. The present study confirms that this residual variability is very consistent over different conditions of breeds and centres.

Conclusion

The model used to analyse the AI results took into account all available information relative to the male, female and to non-sex-specific effects, leading to potentially more precise estimates. To our knowledge, it is the first model that included effects relative to the semen in a joint model of female fertility and male fecundancy. In agreement with the literature, the main variation factors of AI success, evidenced by this joint model, were relative to non-sex-specific effects and to female effect. Nevertheless, semen motility had a small but significant effect. According to these results, choosing females to inseminate might slightly improve the AI results. Heritabilities estimated with this joint model were very low and were lower for male fecundancy than for female fertility. It means that genetic improvement of AI results through a classical polygenic selection would be difficult. In spite of combining a large number of variation factors related to the male and the female, the joint model explained a very small part of the total variability. Perhaps the way to combine the influence of both sexes on the AI results is not additive but multiplicative. New joint product models are being developed in order to go one step further from the joint additive model in the analysis of fertility (David *et al.*, 2007a).

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