Estimation of genetic parameters for litter size after natural and hormone-induced oestrus in sheep

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Abstract

Genetic parameters for litter size after natural and hormone-induced oestrus were estimated for Ovin Ile de France, Blanc du Massif Central and Mouton Vendéen-sheep, using REML methods in animal and sire BLUP models on litter size and normal scores. Litters born after hormone-induced oestrus and after natural oestrus were treated as different traits in order to estimate the genetic correlation between the traits and the genetic parameters of each trait. Explanatory variables were the year*flock*season of lambing effect, the physiological condition factor combining the mode of rearing, age at the first lambing, rhythm of lambing and number of lambs suckled at the previous lambing, the month of birth nested within gestation number, a permanent environmental effect associated with the ewe and the additive genetic effect (sire or animal effect). For the three breeds, the heritability estimates for natural litter size, equal to 0.10, was higher than the heritability estimates for induced litter size, equal to 0.06. The estimate of genetic correlation between the two fecundation types was closed to 0.75. This result suggests that natural and induced litter size can be considered as two traits controlled by a great number of common genes. This genetic correlation was higher than the previous estimation (0.40) reported in Bodin (1979). Nevertheless, the genetic correlations estimates between litter size on first lambing after induced oestrus and the other litter size are not the same for the three breeds, ranging from -0.30 to 1 for Mouton Vendéen and Blanc du Massif Central-sheep respectively.

Keywords : sheep, genetic parameters, litter size, hormone-induced oestrus, natural oestrus

1   Introduction

Litter size is one of the most important components of profitability of suckling sheep farming: it affects more the variability of the weight of weaned lambs per ewe than does the individual growth of the lambs. For some breeding schemes of suckling sheep, litter size is one of the main selection objectives. The use of hormonal treatments (such as a vaginal sponge impregnated with a synthetic analogue of progesterone inserted in the ewe vagina for a 12 or 14-day period with a PMSG injection at withdrawal) required for a better reproduction management and an efficient set up of selection program affects prolificacy. At the present time, in the French genetic evaluation of prolificacy, two different breeding values are estimated for each animal: one for prolificacy after natural oestrus (NO) and another for prolificacy after induced oestrus (IO). These estimations are based on the genetic parameters which were known when this evaluation was set up in 1992 (Institut de l'Elevage, 1995). They were estimated to 0.10 and 0.08 for the heritability of litter size after natural and induced oestrus respectively; 0.20 and 0.15 for the repeatability of litter size after natural and induced oestrus respectively and 0.40 for the genetic correlation between these traits according to the estimation made on the Lacaune breed by Bodin (1979).

The objective of this study was to estimate new values of genetic parameters of prolificacy and specifically the relation between natural and induced litter size in order to

optimise the selection of the global trait prolificacy. Three breeds (Ovin Ile de France, Blanc du Massif Central and Mouton Vendéen-sheep) were considered in this study. Their characteristics are presented in table 1.

Table 1: Characteristics of the studied breeds (year 2002)

		Ovin Ile de France	Blanc du Massif Central	Mouton Vendéen
Total livestock		240 000 females	300 000 females	250 000 females
Controlled livestock		28 151 females	36 760 females	10 093 females
Number of controlled farms		165	113	55
Breeding system		Pen's breed	Hardy breed	Grazier breed
Lambing period		Autumn principally and spring	Winter spring summer (fast reproduction rhythm)	Autumn and spring
Prolificacy after natural oestrus	Lambing before 19 month	1.50	1.32	1.55
	Lambing after 19 month	1.68	1.43	1.70
Prolificacy after induced oestrus	Lambing before 19 month	1.66	1.56	1.76
	Lambing after 19 month	1.83	1.62	1.87
Number of lambing after induced oestrus		2 515 (16%)	4 560 (13%)	1 559 (16%)
Number of lambing with known paternity		10 837 (69%)	10 274 (29%)	7 875 (83%)
Selection scheme		Breeding aptitudes Butcher aptitudes	Breeding aptitudes Butcher aptitudes	Butcher aptitudes Maternal qualities

From: Institut National de la Recherche Agronomique, Institut de l'Elevage, France Upra Sélection, 1997

2 Material and methods

2.1 Animals

Data came from the French national performances recording scheme (French National database). This database holds pedigree information and performance data on prolificacy collected from 1982 to 2002. For each performance of ewe, the number of lamb born, the date of lambing, the flock number, the season of lambing, the gestation number and the mode of reproduction (natural or induced oestrus) are recorded. The database also contents information about the birth of the ewe : birth date, type of birth (single, twin, triplet) and the mode of rearing (single, twin, triplet or artificial rearing). For the three breeds, litter size ranged from 1 to 8, but for the study, only 5 classes were considered, the last class included litter size equal to 5 and more. The performances of ewes entered in the database during their career, those of the ewes without information about their birth and records with obvious errors were removed.

From the original data set, the occurrence of oestrus type per ewe and the number of ewes per sire was not optimal for computing genetic parameters, so different subsets were retained for each breed.

- To estimate the heritability, independent samples were built for prolificacy after natural and induced oestrus. Severe samples were created by keeping only the performances of sire families with at least 30 half-sibs having records in natural oestrus (30_{NO}) and in induced oestrus (30_{IO}). Less severe, but larger samples were also considered by keeping the

performances of sire families with at least 15 and 10 half-sibs having records in natural oestrus (15_{NO} and 10_{NO} respectively) and in induced oestrus (15_{IO} and 10_{IO} respectively).

- To estimate the genetic correlation, subsets with the performances of sire families with at least 30 half-sibs having at least one lambing after natural oestrus and at least 30 half-sibs having at least one lambing after induced oestrus (sample "30_{NO} & 30_{IO}") were generated. Less severe samples were built with performances of smaller sire families with at least 15 and 10 half-sibs in each oestrus type (samples "15_{NO} & 15_{IO} and 10_{NO} & 10_{IO}"). The number of records for each sample and each breed studied are presented in table 2.

Table 2: Number of lambing and family sires in samples selected to estimate genetic correlation between litter size after natural (NO) and induced (IO) oestrus.

Samples[†]	Number of	Ovin Ile de France		Blanc du Massif Central		Mouton Vendéen	
		NO	IO	NO	IO	NO	IO
30NO-30IO	lambing	30 652	11 017	66 026	14 989	39 741	16 366
	ewes	10 470	5 773	15 733	8 560	13 431	8 520
	sires	80		139		169	
15NO-15IO	lambing	52 073	18 717	98 792	22 030	83 299	32 982
	ewes	17 546	9 852	24 267	12 937	27 951	17 263
	sires	274		354		598	
10NO-15IO	lambing	72 599	25 092	117 610	25 314	105 136	40 900
	ewes	24 148	13 317	28 717	14 974	35 419	21 539
	sires	554		526		957	
30NO	lambing	71 637		106 647		88 822	
	ewes	23 651		27 354		29 968	
	sires	395		401		558	
15NO	lambing	119 697		139 697		131 852	
	ewes	39 766		35 355		44 890	
	sires	1 183		785		1 284	
10NO	lambing	138 725		151 385		147 549	
	ewes	46 486		38 115		50 370	
	sires	1 756		1 016		1 748	
30IO	lambing		12 954		14 989		16 366
	ewes		6 479		8 560		8 520
	sires		98		139		169
15IO	lambing		21 373		22 053		33 346
	ewes		10 778		12 952		17 438
	sires		315		355		609
10IO	lambing		27 294		25 346		41 420
	ewes		14 171		14 997		21 778
	sires		605		528		978
40NO-4L	lambing	35 184		77 224		45 010	
	ewes	5 841		11 012		7 375	
	sires	199		254		318	

[†]see text for sample definition

- To estimate genetic parameters at different parities, the same samples were used but they were split in three parts considering gestation number: one subset with the first lambing data, one with the second lambing data and one with data of the other lambing.

- To estimate more closely the additive genetic and the permanent environmental effects, a sample more severe on ewes were considered in using sire families with at least 40 half-sibs having at least 4 lambing after natural oestrus ("40_{NO}-$_{4L}$").

- Finally, to estimate the genetic correlation between prolificacy at first lambing on induced oestrus and those at subsequent natural lambing, samples with records of sire families with at least 15 half-sibs having their first lambing on induced oestrus ("$15_{IO.1}$") were generated for the Ovin Ile de France and Blanc du Massif Central breeds.

2.2 Models

To estimate variance components, linear mixed model methodology on litter size and normal scores (transformed variables) (Poivey *et al.*, 1990 ; 1994) was used. Litters born after induced oestrus and after natural oestrus were treated as different traits in order to estimate the genetic parameters. Using the Mixed procedure of SAS (1999) and the VCE4 software (Groeneveld, 1998), univariate (one model for each oestrus type) and bivariate models with the REML (Restricted Maximum Likelihood estimator, Patterson and Thompson, 1971) method were applied to an animal or a sire model. These linear mixed models included fixed effects routinely used in the French genetic evaluation of the prolificacy for suckling sheep, a permanent environmental effect associated with the ewe and the additive genetic effect (sire or animal effects). The interaction year*flock*season of lambing effect, a physiological condition factor and the month of birth nested within gestation number were taken into account in the fixed part of the model. The "physiological condition" factor represents a combination of mode of rearing, age at the first lambing, rhythm of lambing and number of lambs suckled at the previous lambing (Poivey *et al.*,1995).

3   Results
3.1 Litter size

The means and the variances of the litter size after natural and induced oestrus for the sample 30_{NO}& 30_{IO} are presented in table 3 for each breed.

Table 3: Means (μ) and standard deviation (σ) of the litter size after natural (NO) and induced oestrus (IO) for the three breeds and mean litter size for the first ($μ_{LS1}$), the second ($μ_{LS2}$) and the other ($μ_{LS3+}$) lambing for the OIF and BMC breeds.

	Type of oestrus	Ovin Ile de France	Blanc du Massif Central	Mouton Vendéen
μ		1.64	1.42	1.75
σ		0.60	0.55	0.64
$μ_{LS1}$	NO	1.56	1.35	
$μ_{LS2}$		1.60	1.38	
$μ_{LS3+}$		1.73	1.50	
μ		1.86	1.68	1.96
σ		0.82	0.72	0.78
$μ_{LS1}$	IO	1.73	1.48	
$μ_{LS2}$		1.91	1.67	
$μ_{LS3+}$		1.93	1.73	

The sample size of records after induced oestrus is smaller for all breeds because in suckling sheep, relatively few hormonal treatments are used (table 2), however, the mean prolificacy is very stable among the different samples within breed and within reproduction type. The average litter size after natural oestrus (1.42 in BMC, 1.64 in OIF, 1.75 in VEN) is lower than after induced oestrus (1.68 in BMC, 1.86 in OIF and 1.96 in VEN), but the variability of litter size after induced oestrus is higher. Its standard deviation (0.72 in BMC, 0.82 in OIF and 0.78 in VEN) is increased by about 30% compared to the standard deviation of litter size after natural oestrus (0.55 in BMC, 0.60 in OIF and 0.64 in VEN).

Whatever the mode of reproduction, the average of litter size increases with parity in OIF and BMC breeds (table 3). The mean natural prolificacy is increased by 2.5% in second lambing and then is increased by 8% between the second ant the third and more lambing. This age effect is different after induced oestrus, since there is an higher increase between the first and second lambing (10%) than later (2%). Moreover at each lambing, hormonal treatment results in an increase of prolificacy with a largest effect at the second lambing where difference between natural and induced prolificacy reaches 20%.

3.2 Heritability and repeatability

Estimation of genetic parameters obtained with the different samples are very similar for the three breeds and both the reproduction type. Sire and animal models lead also very close estimated parameters. Estimations of genetic parameters made with the raw litter size or the normal score transformation are very stable. Because results are very close, only estimations of genetic parameters of the sample 30_{NO} & 30_{IO} are presented in table 4 for the three breeds with a univariate sire model and a bivariate animal model on raw litter size, and an bivariate animal model on normal score transformation.

For the three breeds, heritability estimates are very low and similar within each fecundation type using an animal or a sire models (table 4). Heritability of natural prolificacy (h^2_{NO}) ranges from 0.08 in OIF to 0.14 in VEN, while heritability of induced prolificacy (h^2_{IO}) is slightly lower, ranging from 0.05 in VEN to 0.07 in BMC and OIF. The standard errors range from 0.002 to 0.010 and is multiplied by two between the less severe sample "10_{NO} & 10_{IO}" and the most severe one "30_{NO} & 30_{IO}".

Repeatability of the litter size after natural oestrus (equal to 0.12 for the three breeds) is slightly larger than the repeatability of the litter size after induced oestrus, ranging from 0.07 to 0.11 (table 4). These differences in heritability and repeatability are mainly due to a lower residual variance for the performances after natural oestrus whereas the genetic variance is generally upper for the induced prolificacy and the variance of permanent environmental effect are closed.

Heritability of litter size at each parity, which has been estimated for OIF and BMC breeds, generally decreases when ewe get older (table 5). In natural oestrus, heritability decreases slowly between the first and the third and more lambing. In induced oestrus, it is higher at the first lambing than at the second, and higher at the second than at the other lambing (0.12, 0.08 and 0.05 in OIF respectively and 0.16, 0.09 and 0.04 in BMC respectively).

Table 4: Genetic additive (V(a)) animal permanent (V(P)) residual (V(e)) variances, heritability (h^2), genetic correlation (r_g) and repeatability of prolificacy after natural (NO) and induced (IO) oestrus estimated with animal or sire univariate or bivariate models and on observed litter size or after normal score transformation.

Parameter	Model[†]	Ovin Ile de France	Blanc du Massif Central	Mouton Vendéen
V(a) NO	1	0.03	0.03	0.05
	2	0.03	0.03	0.04
	3	0.05	0.06	0.07
V(a) IO	1	0.04	0.04	0.03
	2	0.04	0.03	0.03
	3	0.05	0.04	0.04
V(P) NO	1			
	2	0.02	0.01	0.01
	3	0.03	0.01	0.01
V(P) IO	1			
	2	0.03	0.01	0.02
	3	0.04	0.02	0.02
V(e) NO	1	0.31	0.27	0.37
	2	0.28	0.25	0.33
	3	0.58	0.58	0.63
V(e) IO	1	0.64	0.50	0.58
	2	0.58	0.46	0.54
	3	0.72	0.7	0.75
h^2_{NO}	1	0.09 ±0.006	0.12 ±0.004	0.14 ±0.005
	2	0.08 ±0.005	0.10 ±0.005	0.10 ±0.005
	3	0.08 ±0.006	0.10 ±0.004	0.10 ±0.005
h^2_{IO}	1	0.06 ±0.007	0.07 ±0.005	0.06 ±0.005
	2	0.07 ±0.007	0.06 ±0.005	0.05 ±0.005
	3	0.06 ±0.007	0.06 ±0.005	0.05 ±0.005
$r_{g\ NO\ IO}$	1			
	2	0.73 ±0.081	0.74 ±0.051	0.75 ±0.058
	3	0.74 ±0.080	0.73 ±0.050	0.74 ±0.059
repeatability $_{NO}$	1			
	2	0.12 ±0.006	0.12 ±0.005	0.12 ±0.005
	3	0.12 ±0.006	0.12 ±0.004	0.12 ±0.005
repeatability $_{IO}$	1			
	2	0.11 ±0.007	0.09 ±0.005	0.08 ±0.004
	3	0.11 ±0.007	0.08 ±0.006	0.07 ±0.005

[†]**1** : univariate sire model on raw litter size
 2 : bivariate animal model on raw litter size
 3 : bivariate animal model on normal scores

Table 5: Heritability estimates and its standard errors of the litter size after natural and hormone-induced oestrus according to parity

		1st lambing	2nd lambing	3td lambing
Ovin Ile de France	h^2_{NO}	0.10 ±0.02	0.08 ±0.02	0.09 ±0.02
	h^2_{IO}	0.12 ±0.05	0.08 ±0.05	0.05 ±0.02
Blanc du Massif Central	h^2_{NO}	0.17 ±0.02	0.14 ±0.02	0.10 ±0.01
	h^2_{IO}	0.16 ±0.08	0.09 ±0.04	0.04 ±0.01

3.3 Genetic correlation between litter size after natural and induced oestrus

The genetic correlation between litter size after natural and induced oestrus was estimated with an animal and a sire models for the three breeds and by using different subsets of data. Whatever the samples used, results are very stable and closed with values varying from 0.70 to 0.74 in OIF, 0.73 to 0.76 in BMC and 0.74 to 0.79 in VEN (table 4).

3.4 Genetic correlation between litter size at the first lambing after induced oestrus and the other litter sizes

The genetic correlations estimated between the litter size at the first lambing after induced oestrus and adult litter sizes at the other lambing after induced estrus (rg $_{IO.1\ IO.X}$) or after natural oestrus (rg $_{IO.1\ NO.X}$) are different according to the breeds (table 6).

Table 6: Heritabilities and genetic correlation between litter size at the first lambing after induced oestrus and the other litter sizes

	$IO.1_I$	$h^2_{IO.1}$	IO.X	$h^2_{IO.X}$	Rg $_{IO.1\ IO.X}$	NO.X	$h^2_{NO.X}$	rg $_{IO.1\ NO.X}$
OIF	1.69	0.19 ±0.031	1.88	0.08 ±0.011	0.91 ±0.060	1.67	0.06 ±0.008	0.53 ±0.103
BMC	1.43	0.12 ±0.049	1.69	0.07 ±0.013	1.00 ±0.000	1.45	0.11 ±0.005	0.99 ±0.092
VEN	1.74	0.16 ±0.093	1.98	0.03 ±0.011	0.10 ±0.265	1.81	0.10 ±0.015	-0.30 ±0.141

IO.1 : Average of the litter size at the first lambing after induced oestrus
IO.X: Average of the litter size at the second and more lambing after induced oestrus
NO.X: Average of the litter size at the second and more lambing after natural oestrus

In BMC breed, the genetic correlations between induced first litter size and the adult litter sizes either after natural or induced oestrus are closed to 1. In OIF breed, genetic correlations of the induced first litter size are equal to 0.91 with the induced adult prolificacy and equal to 0.53 with the natural adult prolificacy. Nevertheless, these same genetic correlations are very low in VEN breed : 0.10 with the adult induced prolificacy and negative (-0.30) with the adult natural prolificacy. These results should be taken cautiously. The sample size for performances after induced oestrus is generally smaller for all breeds because in suckling sheep, few hormonal treatments are used (table 2). Moreover in many breeding schemes, the first mating is recommended to be on natural oestrus.

4   Discussion and conclusion

The higher variability of induced prolificacy compared to natural prolificacy observed in these three breeds agrees with previous studies on the same breeds as well as on other French breeds. This variability increase is larger than the scale effect due to the increase of mean prolificacy, as reported by Bodin and Elsen (1989). In natural oestrus, increase of prolificacy with age is well known, but the effect of hormonal treatment with age is less documented.

Hormonal treatment seems to smooth the age effect. After induced oestrus, the mean prolificacy reaches a plateau earlier than after natural oestrus and the fast increase occurs at a younger age.

The model describing natural or induced prolificacy contains fixed effects corresponding to correction factors used routinely in the French genetic evaluation of the prolificacy for suckling sheep (year*flock*season of lambing effect, a combination of mode of rearing, age at the first lambing, rhythm of lambing and number of lambs suckled at the previous lambing and the month of birth nested within gestation number), a permanent environmental effect associated with the ewe and the additive genetic effect (sire or animal effects). This model only explains 18% of the total variance. In order to improve the predictability of the model, other factors such as the number of lambs suckled at the previous lambing, the mode of suckling of the ewe, the mode of birth of the ewe could be included. These factors have been tested in previous analysis but they are not taken into account to the genetic evaluation model because the estimated effects of these factors are different from the zootechnical reality. These discrepancies are due to problems of confusion between positive genetic and negative non-genetic effects gathered by these variation factors. For the French genetic evaluation, Poivey (1990) chose to consider these effects in the "physiological condition" factor when the negative effect is large (i.e. for the youngest ewes of those with a short post partum delay fast reproduction rhythm). An other factor such as the dose of PMSG administrated could also be included in the genetic evaluation model. At the present time, this information is not recorded.

Several samples were built in this study to estimate genetic parameters of the litter size after natural and induced oestrus. Several studies have shown that data structure (quality and quantity of data) and absence of connectedness can affect the estimation and the precision of genetic parameters. The results obtained in this study are very stable between samples, this can be explained by a good connectedness between flocks and a sufficient quantity of information.

The aim of this study was to obtain new estimations of genetic parameters for natural and induced prolificacy (h^2, r_g) in order to optimise the global selection of the trait. Heritability estimated for all the lambing on natural oestrus (0.10) agreed with the results of recent studies (Janssens *et al.*, 2004). Matos et al. (1997) find a heritability of 0.16 in Rambouillet and of 0.08 in Finnsheep, Altarriba *et al.* (1998) a heritability of 0.08 in Rasa Aragonesa. Only Lee *et al.*, (2000) estimate a lower heritability (0.05) in Rambouillet. Repeatability of natural prolificacy is relatively low in our study and lower than that found by Janssens *et al.* (2004). However our results are very stable regarding to the different breeds and samples, even on the restricted sample with large families (40 daughters with at least 4 litters each). Estimation of heritability of induced oestrus also agrees with previous (Bodin, 1979) and recent results (Janssens *et al.*, 2004), although for these last authors the values of heritability on induced oestrus are very close to that of natural prolificacy. In our study, heritability of induced prolificacy is slightly lower than for natural prolificacy mainly due to a higher residual variance.

The genetic correlation estimated in this paper (0.75) is higher than the previous estimation (0.40 in Bodin, 1979) used at the present time in the French genetic evaluation of prolificacy. However this estimation (0.40) was done only on first lambing of dairy Lacaune ewes with a more simple method based on correlation between breeding values for each trait. This new estimation of the genetic correlation (0.75) agrees with those of Janssens *et al.* (2004) got on Texel and Suffolk breeds by an animal REML model.

The stability of the estimation of genetic parameters (heritabilty, repeatability and genetic correlation) obtained in this study involves to take into account the same model and the same genetic parameters for each breed analyzed.

This study also underlines the fact that heritability of prolificacy on the first parity are higher than those estimated at older age. This result agrees with the estimation of Gates and Urioste (1995) on Swedish ewes in which heritability of the prolificacy is higher at the first lambing and after decreases. Nevertheless, Yadzi *et al.* (1999) and Lee *et al.* (2000) find that heritability of the prolificacy increases from the first to the third lambing. Contrary to the other results, genetic correlations between prolificacy at the first parity on induced oestrus and

prolificacy at the other parities on natural or induced oestrus are different according to the breeds. In view of these differences and the size of the samples, these results required additional analyses.

A new value (0.75) for the genetic correlation will be included in the computations of the breeding values and the determination coefficient of suckling-sheep. Moreover, selection for the litter size is based on a synthetic breeding value combining the estimation of both breeding values weighed by coefficients. At the present time these coefficient are the proportion of each reproduction (natural or induced) in each breed. They should be changed according to the real economic weight of each reproduction in the selection objectives.

5 Acknowledgements

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