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Multiple-trait genetic parameters and genetic evaluation of udder-type traits in Lacaune dairy ewes

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Abstract

Genetic parameters for three linear udder-type traits (teat angle, udder cleft and udder depth) in the Lacaune breed were estimated by restricted maximum likelihood (REML) using a multiple-trait animal model. The analyses were carried out on 82,019 primiparous ewes in 352 flocks, recorded by 12 classifiers from 2000 to 2003. Estimated breeding values (EBV) were computed for udder-type traits and correlations between EBV for udder-type traits, EBV for milk yield and somatic cell scores were examined. Heritability estimates were 0.19 for udder depth, 0.26 for udder cleft and 0.33 for teat angle. The genetic correlations among udder traits were globally moderate to high (ranging from 0.14 to 0.49) and always favourable. Over the last 5 years, the trends of EBV showed a deterioration of udder-type traits, especially for udder depth. Most correlations between EBV for type traits and EBV for milk traits were weak. The correlations of the combined index with udder cleft and teat angle were close to zero while that of udder depth with the former was -0.29 , confirming the EBV trends. In addition, the correlations between EBV for somatic cell scores and EBV for udder-type traits were weak but favourable (from 0.1 to 0.2). © 2005 Elsevier B.V. All rights reserved.

Keywords: Dairy sheep; Lacaune sheep; Genetic parameters; Genetic evaluation; Udder-type traits; Type appraisal

1. Introduction

Since the 1990s, breeders of Lacaune sheep have complained about damage of the ewe's udder mor-

phology and reported an increasing number of "baggy udders." The improvement of udder conformation might be beneficial to milking ability and animal health, but present selection on dairy production traits does not warrant a favourable trend in udder morphology. Marie (1999b) showed an unfavourable association between milk yield selection and udder shape of Lacaune divergent lines, while milk flows are improved by selection for milk yield (Marie-Etancelin

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et al., submitted for publication). Since the selection scheme of the Lacaune dairy breed achieves an annual gain on milk yield of about 6 l (Astruc et al., 2002), Lacaune sheep breeders decided to gradually include udder morphological traits in the selection index. Previous studies in Lacaune ewes have allowed for the identification of basic and repeatable traits, which are suitable to the characterisation of udder conformation (Marie-Etancelin et al., 2001). Similar appraisal methods have been used in Spain (Fernandez et al., 1997; Ugarte et al., 2001; Serrano et al., 2002) and in Italy (Carta et al., 1999; Casu et al., 2002), but with some differences in the analysed traits. Since 1999 in France, the proposed appraisal method based on three udder-type traits (teat angle, udder cleft and udder depth) has been applied in the Lacaune nucleus flocks, and classifiers have been trained accordingly. In 2003, about 90% of the Lacaune nucleus flocks had primiparous ewes scored on udder-type traits.

The aim of this study was, first, to estimate the genetic parameters of teat angle, udder cleft and udder depth in Lacaune dairy sheep, and secondly, to compute estimated breeding value (EBV) for udder-type traits and to estimate the correlation of EBV for udder traits with currently selected traits such as milk yield, milk composition and somatic cell counts.

2. Materials and methods

2.1. Data

From 2000 to 2003, 12 technicians of the French Lacaune Association and the two artificial insemination (AI) centres, collected records on udder-type traits. These trained classifiers scored three traits according to a linear scale (from 1 to 9), which allowed the application of statistical methods for continuous traits. These three recorded traits described in Fig. 1 were the following: the first one was teat angle (TA) as the angle between the vertical line and the right teat axis, the second one was udder cleft (UC) as the degree of separation of the two halves (appraised as a combination of the angle and the height of the cleft in order to express the strength of the suspensor ligament), and the third one was udder depth (UD) as the distance between the abdominal wall and the udder floor (taking as a reference the height of the

Teat Angle	Udder Cleft	Udder Depth
1 = vertical 9 = horizontal	1 = missing 9 = well marked	1 = deep 9 = shallow

Fig. 1. Description of the three linear udder traits.

hocks in order to consider differences in animal size). Udder balance, as an appraisal of the symmetry of the two halves, (four levels) was collected in order to remove from the data set records of strongly unbalanced udders mainly reflecting sanitary problems.

The data originated from Lacaune flocks of the French nucleus breeding scheme. A sample of 82,019 Lacaune ewes, recorded in first lactation at 1 year of age, was available after removing animals with unbalanced udders (about 4% of total data set). The records were from 352 flocks, representing 90% of the nucleus of the French breeding scheme. The number of flocks and classifiers increased from 2000 to 2003 (Table 1). For each animal, the data available were the following: year, flock, classifier, stage of lactation, age at lambing, time between previous milking and scoring, number of suckling lambs. The data analysed included performance records on 82,019 ewes sired by 2486 Lacaune rams for three type traits. Each sire had at least 20 recorded daughters and each classifier had scored at least 2900 ewes.

2.2. Statistical analysis

2.2.1. Model

The data were analysed using the following multiple-trait animal model:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{a} + \mathbf{e}$$

where \mathbf{y} is a vector of n observations for all traits T ; $\boldsymbol{\beta}$ is a vector of fixed effects; \mathbf{a} is a random vector of additive genetic effects; \mathbf{e} is a random vector of residual effects; and \mathbf{X} and \mathbf{Z} are incidence matrices

Table 1
Description of data set

Years	2000	2001	2002	2003	Total
Flocks	60	223	305	343	352
Classifiers	5	10	12	12	12
Recorded ewes	5847	19,822	26,808	29,542	82,019

relating records to their respective effects, as to say fixed and random genetic effects. These two incidence matrices are identical for all three traits. The assumptions of the model are

$$E(\mathbf{a}) = E(\mathbf{e}) = \mathbf{0} \quad \text{and} \quad E(\mathbf{y}) = (\mathbf{I}_T \otimes \mathbf{X})\boldsymbol{\beta}$$

with variances and covariances

$$\text{Var} \begin{bmatrix} \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A} \otimes \mathbf{G} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}_n \otimes \mathbf{R} \end{bmatrix} \quad \text{and}$$

$$\text{Var}(\mathbf{y}) = \mathbf{ZAZ}' \otimes \mathbf{G} + \mathbf{I}_n \otimes \mathbf{R}$$

where \otimes denotes the direct product between two matrices; \mathbf{A} is the numerator relationship matrix; \mathbf{I}_T and \mathbf{I}_n are identity matrices; \mathbf{G} and \mathbf{R} are the genetic and residual variance–covariance matrices between the three traits for the additive genetic and the residual effects, respectively. Pedigrees were traced back up to seven generations of ancestors on male and female sides. The complete pedigree file included 247,508 animals, including the 82,019 scored ewes.

The factors of variation considered were year (4 levels); flock (352 levels); classifier (12 levels); class of lactation stage (6 levels: less than 50 days, between 51 and 75 days, between 76 and 100 days, between 101 and 125 days, between 126 and 150 days, more than 151 days); class of age at lambing (4 levels: less than 370 days, between 370 and 400 days, between 400 and 420 days, more than 420 days); class of time for udder filling, i.e., time between previous milking and scoring (four levels: less than 360 s, between 360 and 550 s, between 550 and 700 s, more than 700 s); and number of suckling lambs (three levels: one suckling lamb, two suckling lambs, three or more suckling lambs). Preliminary analyses showed significant effects for year, flock, classifier and time for udder filling combinations (931 levels), for year, stage of lactation and age at lambing combinations (63 levels), for year and number of suckling lambs (12 levels). Consequently, the vector $\boldsymbol{\beta}$ included these three com-

binations of fixed effects, which are described in Table 2.

2.2.2. Genetic parameter estimation

A multiple-trait restricted maximum likelihood (REML) estimation was carried out on the three udder-type traits. Since the same model was applied to all traits, with no missing data, residual and genetic variance–covariances were estimated using a canonical transformation (Meyer, 1985) applied to an animal model. Standard errors of estimates of heritabilities, genetic and residual correlations were computed as in Colleau et al. (1989).

The calculations were greatly alleviated by first computing the eigenvalues of the fixed effect part of the coefficient matrix, using the Cullum and Willoughby (1985) technique by reducing a large sparse symmetric matrix to a tridiagonal matrix. Then, the traces of inverses of the coefficient matrices on the canonical scale that are repeatedly required in the Fisher-scoring REML iterative procedure are obtained in linear time, as described by Robert and Ducrocq (1996). In the second step, the REML estimation, using the Fisher-scoring procedure (Ducrocq, 1993), was easier to perform with few memory requirements: convergence was obtained after 12 iterations. Programmes to perform these two steps of genetic parameter estimation were written in Fortran by Ducrocq and Robert-Granić (personal communication).

With these programmes, estimates of heritabilities of each udder conformation traits, genetic and residual correlations between these udder traits were obtained.

2.2.3. Genetic evaluation

Estimated breeding values (EBV) were computed simultaneously for the three udder-type traits, using best linear unbiased prediction (BLUP) applied to the multiple-trait animal model previously described. The genetic evaluation estimation was performed using the

Table 2
Description of the combination of fixed effects

Fixed effects	Levels	Records per levels of effects		
	<i>N</i>	Mean	Minimum	Maximum
Year × flock × classifier	931	88	15	410
Year × (lactation stage × date of lambing)	63	1302	30	7933
Year × number of lambs	12	6835	159	18,301

BLUPF90 program, kindly provided by Mizstal et al. (2002). The reliability of predicted breeding values is commonly assessed by the so-called coefficient of determination (CD) that is the squared correlation between the true and estimated genetic values. In theory, CD is derived from the elements of the inverse of the coefficient matrix of the mixed model equations. In practice, the number of animals to be evaluated is generally too large to invert this coefficient matrix and the elements of the inverse have to be approximated. Here, the approximation developed by Harris and Johnson (1998) was used.

Genetic trends were estimated by averaging udder EBV for females and males (with a reliability over 0.30) by birth year from 1997 to 2002. Sample size depending on the trait, from 2091 to 2287 males and from 78,250 to 93,329 females.

2.2.4. Relationships between EBV for udder traits, EBV for milk traits and EBV for somatic cell scores

Currently, official breeding values computed in France for dairy sheep breeds concern EBV for milk production traits (milk yield, fat content, protein content and selection criteria—as a combination of the EBV of the previous traits) as described by Astruc et al. (2002) and EBV for somatic cell scores as described by Rupp et al. (2002). Correlations between EBV for milk production traits and somatic cell score on one hand, and EBV for udder-type traits on the other, were estimated for 1092 progeny tested Lacaune rams with at least 10 recorded daughters.

3. Results and discussion

3.1. Basic statistics

Averages for the three udder traits (teat angle, udder cleft and udder depth) are presented in Table

Table 3
Description and elementary statistics of udder traits

Traits	Description		Elementary statistics		
	1	9	Mean	S.D.	CV (%)
Teat angle (TA)	Vertical	Horizontal	6.74	1.12	17
Udder cleft (UC)	Absent	Marked	4.99	1.32	26
Udder depth (UD)	Deep	Shallow	6.54	0.68	10

Table 4
Heritabilities (and standard errors) [on diagonal], genetic correlations (and standard errors) [above the diagonal] and residual correlations (and standard errors) [under the diagonal]

	Teat angle	Udder cleft	Udder depth
Teat angle	0.33 (0.01)	−0.37 (0.03)	−0.49 (0.03)
Udder cleft	−0.14 (0.02)	0.26 (0.02)	+0.14 (0.04)
Udder depth	−0.03 (0.03)	+0.11 (0.03)	0.19 (0.01)

3. Scored primiparous ewes tended to have a teat angle (TA) close to 90° with a minimum value always higher than 3. A TA score of 6.74 points corresponded to about 75° between the teat and the vertical line, which is very unfavourable for milking, especially for plugging the cluster. The udder cleft (UC) was on the average (5), but UC was the more variable morphological trait (26% for UC rather than 10% for UD to 17% for TA), using the whole scale from 1 to 9. Since the appraisals were done on first-lactation ewes, the udder depth (UD) was small, on average 5–10 cm above the hocks, less variable, with individual data always higher than 2. Similar values were observed for the same breed under experimental conditions (Marie et al., 1999a).

Comparisons between udder mean values among different appraisal tables (Spanish, Italian or French) must be considered with caution. First, the French approach of udder morphology deletes unbalanced udder data, whereas the other approaches take all data into account. Second, the scoring of the same ewes with Italian and French appraisal tables revealed a discrepancy from 0.3 points for TA to 1.2 points for UC (Marie-Etancelin et al., 2002). However, since correlations between Italian and French classifiers showed a great likeness between teams for UD and TP (mean correlation about 0.79) and to a lesser extent for UC (mean correlation about 0.68), comparisons of genetic parameters were possible.

3.2. Genetic parameters of udder traits

Heritability estimates of linear udder-type traits were generally moderate, ranging from 0.19 for UD to 0.33 for TA, while UC had an intermediate heritability value of 0.26 (Table 4). These results are coherent with repeatabilities reported previously for the Lacaune breed (varying from 0.59 for UD to 0.66 for TA (Marie et al., 1999a)). Moreover, the heritability

estimates in this study were in agreement with the estimates for other sheep breeds. Estimates for udder-type traits ranged from 0.20 to 0.37 for TA (Fernandez et al., 1997; Ugarte et al., 2001; Casu et al., 2002; Serrano et al., 2002), from 0.16 to 0.25 for UD (Fernandez et al., 1997; Ugarte et al., 2001; Casu et al., 2002; Serrano et al., 2002) and equal to 0.19 for UC (Casu et al., 2002). Heritability estimates published in the dairy goat (Luo et al., 1997; Manfredi et al., 2001) and in dairy cattle (DeGroot et al., 2002; Ducrocq, 1993; Short and Lawlor, 1992) were consistent with our heritability estimates in dairy ewes: TA values around 0.35 in the goat and ranging from 0.23 to 0.52 in cattle, and with smaller UD values ranging from 0.25 to 0.34 in the goat and from 0.23 to 0.25 in cattle. Whatever the studies, TA was the trait with the largest genetic variability, which could be useful in breeding programmes in order to improve udder suitability to machine milking.

Genetic correlations among udder traits were all favourable regarding milking ability; that is, the more vertical the TA, the shallower the UD, and the more marked the UC. Moreover, genetic associations were generally moderate to high, with absolute values ranging from 0.14 to 0.49 (Table 4). These results imply that selection based on some of these udder morphological traits will have a positive impact on the global udder morphology. More precisely, selection against the horizontal teat would produce an indirect response towards “baggy udders”.

In order to discuss these results regarding genetic components estimated in appraisal tables from other countries, the scale directions of each trait (TA, UC and UD) need to be remembered (Marie-Etancelin et al., 2001). Genetic correlations between TA and UD were mainly the highest, equal to -0.49 in this study and varying from -0.32 to -0.58 (Fernandez et al., 1997; Ugarte et al., 2001; Casu et al., 2002), except for Serrano et al. (2002) where TA and UD seemed independent. The Italian estimations of genetic correlations (Casu et al., 2002) were close to those of our results for UC-UD ($+0.11$ vs. $+0.14$ in the present study), while a little weaker for UC-TA (-0.17 vs. -0.37 in the present study).

These results—moderate heritabilities and favourable genetic associations between udder traits—allow performing selection on the three udder traits with large gains on each of the three traits. Moreover, a selection on only one udder-type trait will improve the two other udder traits, i.e., the general udder shape. So, a multiple-trait genetic evaluation was done on the three udder-type traits.

3.3. Genetic evaluation

Genetic trends estimated for the three udder traits are illustrated in Fig. 2. From 1997 to 2001, udder depth EBV significantly decreased both for males and females, with a mean fall of 0.5 genetic standard deviations per 10 years. The decreasing trends in the

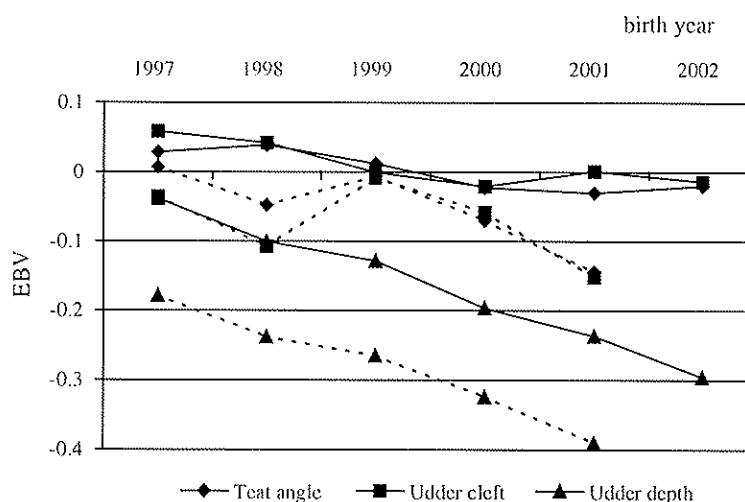


Fig. 2. EBV trends for males (dotted line) and females (continuous line) by birth year (CD > 0.30).

EBV for teat angle and udder cleft were smaller, with an average gradient of about -0.15 genetic standard deviations per 10 years. Since data spanned a limited period, the EBV trends over time were not strongly marked: only udder depth appeared to be deteriorating in males as well as in females.

3.4. Relationships between EBV for udder traits, milk traits and somatic cell scores

Correlations between udder trait EBV and milk trait EBV computed for progeny tested rams were variable and low (Table 5). Fat and protein content EBV were not related to udder conformation EBV, while milk yield EBV was negatively related to udder depth (-0.21), but correlations with teat angle and udder cleft were close to zero. Regarding the literature published for dairy sheep, genetic correlations between milk yield and udder traits were moderate: unfavourable absolute values ranging from 0.02 to 0.82 in Churra (Fernandez et al., 1997) and from 0.01 to 0.46 in Sarda (Carta et al., 2001). The highest correlation value was always obtained with udder depth, which is an obvious indicator of udder volume and milk yield. This result was in agreement with those of the present study.

Regarding the current combined selection criteria on milk production traits—a linear combination of milk yield, fat content and protein content—the unfavourable relationship with udder depth was higher than for milk yield (respectively -0.29 and -0.21) (Table 5). A weak unfavourable association remained between the current combined selection criteria and teat angle ($+0.11$) while the udder cleft became independent

from selection criteria. The present results were in accordance with those observed by Marie (1999b) on two experimental divergent Lacaune ewe lines. This divergent selection for milk yield, which reflected the impact of 10 years of milk selection in the Lacaune breed, showed significant differences between lines for udder depth (5%) and teat angle (4%), but no significant differences for udder cleft. Thus, a larger data set with on-farm records also shows that the current selection on milk yield might damage udder morphology.

Correlations between somatic cell score EBV and udder trait EBV were moderate and favourable (from 0.10 to 0.21): the more adequate the udder morphology (vertical TA, shallow UD and marked UC), the less somatic cell score. In other words, a selection on udder traits would not damage udder health. Such a result was original in dairy sheep but in agreement with dairy cattle literature. Genetic correlations between udder-type traits and somatic cell scores reported by Boettcher et al. (1998) and Rupp and Boichard (1999) were consistent with our genetic correlations estimates: it showed that deep udders and udders with high teat placement were associated with increasing somatic cell scores (values ranging from, respectively, 0.26 to 0.40 for UD and 0.07 to 0.14 for TA).

4. Conclusion

Type appraisal traits, recorded once on primiparous ewes, have intermediate heritabilities in the Lacaune breed. This suggests that simplified recording procedures based on a single scoring per ewe and per lactation on three udder-type traits are able to yield genetic progress. A genetic evaluation on these traits might be implemented in routine, and udder shape could be included in the selection criteria.

The genetic antagonisms between udder conformation and milk production suggested the necessity to include the udder-type traits in the current selection criteria in order to stop at least the worsening of the udder shape. Moreover, genetic relations among udder traits and between udder traits and somatic cell count showed favourable associations. This suggests the possibility to combine these four traits for conformation and health in a global udder selection index. The

Table 5
Correlations between EBV for udder traits and EBV for milk production and somatic cell score ($n = 1092$ sires)^a

	Milk yield	Fat content	Protein content	Selection criteria ^b	Somatic cell score
Teat angle	+0.09	0.05 (ns)	-0.03 (ns)	+0.11	+0.10
Udder cleft	+0.08	-0.14	-0.04 (ns)	-0.02 (ns)	-0.21
Udder depth	-0.21	-0.01 (ns)	-0.02 (ns)	-0.29	-0.21

^a In bold $p \leq 0.001$.

^b Selection Criteria = $1/2$ (Fat Quantity + 1.85 Protein Quantity) + $1/5$ Protein Content.

moderate to weak genetic antagonisms between udder conformation and milk traits suggests the possibility to find a compromise in order to simultaneously improve udder conformation and udder health with an acceptable loss of genetic gain for milk production traits. Genetic trends on each of the three components of the proposed selection criteria will depend on the economic value estimated for udder morphology regarding udder health and milk production trait.

To tackle the whole components of the machine milking ability of Lacaune dairy ewes, genetic relationships between milk flow and udder conformation should be estimated as well as the genetic links between milk flow and somatic cell count.

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