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Estimation of genetic parameters of preweaning performance in the French Limousin cattle breed

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Summary – Direct and maternal genetic and environmental parameters of preweaning growth and conformation at weaning were estimated in the French Limousin beef cattle field recording program using the tilde-hat approach of Van Raden and Jung (1988) with a sire, maternal grandsire (MGS) and dam within MGS model. The numerator relationship matrix among bulls was included in the estimation. The data available after editing contained 169 391 calves with performance records, from 43 683 dams, 7 265 sires, 5 664 maternal grandsires and 1 605 herds, for the years 1972–1989. The traits involved were: birth, 120-d and 210-d weights, average daily gains from birth to 120-d, from 120-d to 210-d, from birth to 210-d, muscular development (MD) and skeletal development (SD) scores at weaning. Estimates ranged from 0.22 to 0.32 for additive direct heritabilities and from 0.06 to 0.16 for maternal heritabilities. Correlations between direct and maternal genetic effects for these traits were negative, ranging from −0.23 to −0.49. Maternal permanent environmental effects were small for all traits, accounting for 5–9% of the phenotypic variances for preweaning growth performance, and 3% and 4% for MD and SD, respectively.

beef cattle / variance components / preweaning growth / conformation score / direct and maternal effects / field data

Résumé – Paramètres génétiques des performances avant sevrage en race bovine Limousine française. *Les paramètres génétiques et environnementaux de la croissance avant sevrage et de la conformation au sevrage ont été estimés pour la race Limousine à partir des données du contrôle de performances en ferme. La méthode d'estimation de ces paramètres était la méthode tilde-chapeau de Van Raden et Jung (1988), avec un modèle père, grand-père maternel et mère intra-grand-père maternel. Les coefficients de parenté ont été inclus dans l'analyse. Les données analysées comprenaient 169 391 veaux avec*

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performances nés entre 1972 et 1989, issus de 43 683 mères, 7 265 pères, 5 644 grand-pères maternels et 1 605 troupeaux. Les caractères considérés étaient : les poids à la naissance, à 120 j et à 210 j, les croissances de la naissance à 120 j, de 120 j à 210 j et de la naissance à 210 j, les développements musculaire et squelettique. Les héritabilités estimées se situent entre 0,22 et 0,32 pour les effets directs et entre 0,06 et 0,16 pour les effets maternels. Les estimées des corrélations génétiques entre effets directs et maternels pour ces mêmes caractères sont toutes négatives et se situent entre −0,23 et −0,49. Les effets d'environnement permanent maternel sont faibles pour tous les caractères, contribuant à la variance phénotypique à hauteur de 5% à 9% pour les caractères de croissance avant sevrage, et de 3% et 4% pour les développements musculaire et squelettique.

bovins à viande / composantes de la variance / croissance avant sevrage / conformation / effets direct et maternel / contrôle de performances en ferme

INTRODUCTION

Knowledge of the magnitude of the variance and covariance components is critical for the genetic evaluation of animals and the development of sound breeding programs. For maternally influenced traits, direct as well as maternal effects need to be quantified. Direct and maternal effects seem to be correlated, but the sign and magnitude of this correlation is often a topic of some debate.

For the estimation of (co)variance components REML (Patterson and Thompson, 1971) is now the method of reference, due to its desirable properties, *ie* non-negativity (Harville, 1977), ability to take account of selection (Sorensen and Kennedy, 1984; Werf and Boer, 1990). With large data sets, however, REML is almost unusable due to the need for inversion of the large coefficient matrix of the mixed model equations (Henderson, 1973) or the inverse of the complete covariance matrix of the vector of observations, despite a number of available numerical techniques (Meyer, 1990). Consequently, less expensive procedures with estimators reasonably close to REML solutions are desirable. Among approximate REML procedures like Henderson's method IV (Henderson, 1980), Schaeffer's method (Schaeffer, 1986) and the tilde-hat approach of Van Raden and Jung (1988), the last has been shown to yield estimates closest to REML solutions in data without or with little selection (Van Raden and Jung, 1988; Ouweltjes *et al*, 1988). Moreover, the tilde-hat approach of Van Raden and Jung (1988) does not require any inversion of a large matrix and is computationally easy even when the numerator relationship matrix and covariances between random effects are included (Manfredi, 1990; Manfredi *et al*, 1991). In the French Limousin breed, genetic trends for preweaning traits have been estimated by an animal model (Laloë, personal communication). It appears that there has been only limited selection practised in the population. With a small data set, Shi and Laloë (1991) showed that the tilde-hat approach led to estimates comparable to those of REML.

The objective of this study was to estimate direct and maternal genetic and environmental parameters for preweaning weights, growth rate and conformation at weaning for the French Limousin cattle breed using the tilde-hat approach of Van Raden and Jung (1988).

MATERIALS AND METHODS

Data description

The French Limousin Breeding Association (France Limousin Selection) provided an extensive data set for estimation of direct and maternal (co)variances for the entire breed in France. Data consisted of 309 530 records collected from 1972 to 1989.

Traits analysed were birth, 120-d, 210-d weights, average daily gain from birth to 120-d (G_{0-120}), from 120-d to 210-d ($G_{120-210}$), from birth to 210-d (G_{0-210}), muscular development (MD) and skeletal development (SD) scores at weaning. The 120-d and 210-d weights were computed by interpolation between neighbouring records which were measured, at 3-month intervals, by technicians according to national rules (FNOCPAB-ITEB, 1983) Some weight records may be used in interpolation for both standard weights. Birth weight, declared by the breeder, was not used in this interpolation. MD and SD were linear functions of elementary scores given by experienced technicians.

Primary edits were conducted by eliminating: 1) calf weights and scores outside 3.5 SDs from the mean values of the corresponding traits within each sex; 2) any calf with a common sire and maternal grandsire (MGS); and 3) calves born from a dam < 23 months or > 16 y old at calving, or later than the 12th parity. Further edits were performed to require, sequentially, sires to have at least 4 progeny, dams to have 2 progeny and MGS to have sired 2 dams, respectively. Herds were required to have a minimum of 8 records. In this way, the edited data set consisted of 169 391 records. For average daily gain traits, only 168 980 records were left after removal of records outside 3.5 SDs from mean values by sex. As a result, 2 data files were used. Further statistics of the data sets are given in tables I and II.

Table I. Characteristics of the French Limousin data sets used for analyses.

Traits	*No. of calves*	*Mean*	*SD*	*Minimum value*	*Maximum value*
Weights (kg):					
Birth weight	169 391	38.0	3.5	26.0	50.0
120-d weight	169 391	158.5	20.8	92.0	232.0
210-d weight	169 391	251.1	33.7	148.0	372.0
Average daily gains (g/d):					
G_{0-120}	168 980	1 004	165	408	1 683
$G_{120-210}$	168 980	1 030	197	344	1 844
G_{0-210}	168 980	1 015	155	505	1 610
Conformation (total score / 100):					
Muscular development	169 391	60.0	8.0	35.0	87.0
Skeletal development	169 391	60.3	6.5	40.0	80.0

Table II. Number of levels and number of records by effects.

Effect	*No.*
Sires	7 265
Maternal grandsires [a]	5 664 (3 529)
Dams	43 683 [d]
Herds	1 605
Herd × year × season [b]	31 513 [d]
Sex	2
Age of dam-parity [c]	9
Calves with record	169 391

[a] Bulls identified at both sire and maternal grandsire; [b] 6 bimester seasons were identified (Jan to Dec by 2-month intervals); [c] 9 age of dam-parity groups were defined according to observed trends; 4 levels for the first parity according to the age of dam (23–29, 30–35, 36–39 and 40–48 month old) and 5 levels for the later parities (2nd, 3rd, 4th–7th, 8th–9th and 10th–12th); [d] 43 682 dams and 31 469 herd–year–season levels for average daily gain traits.

METHODS

A sire, MGS and dam within MGS model was used for estimating the (co)variance components of the assumed maternally influenced traits. The model in matrix notation was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{u}_1 + \mathbf{Z}_2\mathbf{u}_2 + \mathbf{Z}_3\mathbf{u}_3 + \mathbf{e}$$

where:

$\mathbf{y}$ = vector of observations;

$\mathbf{b}$ = vector of unknown fixed effects, including herd-year-season, sex and parity;

$\mathbf{u}_1$, $\mathbf{u}_2$ and $\mathbf{u}_3$ = vectors of unknown random effects for sire, MGS and dam within MGS effects, respectively;

$\mathbf{e}$ = vector of random residual effects;

$\mathbf{Z}$, $\mathbf{Z}_1$, $\mathbf{Z}_2$ and $\mathbf{Z}_3$ = known matrices relating records to the fixed and random effects in the model.

Identification and distribution of the number of levels for the fixed effects are reported in table II.

The expectations and variance–covariance structure of the effects of the model were assumed to be:

$$\mathbf{E}\begin{bmatrix}\mathbf{y}\\ \mathbf{u}_1\\ \mathbf{u}_2\\ \mathbf{u}_3\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{Xb}\\ 0\\ 0\\ 0\\ 0\end{bmatrix} \quad \mathrm{Var}\begin{bmatrix}\mathbf{y}\\ \mathbf{u}_1\\ \mathbf{u}_2\\ \mathbf{u}_3\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{V} & \mathbf{Z}_1\mathbf{A}\sigma_1^2 + \mathbf{Z}_2\mathbf{A}\sigma_{12} & \mathbf{Z}_2\mathbf{A}\sigma_2^2 + \mathbf{Z}_1\mathbf{A}\sigma_{12} & \mathbf{Z}_3\sigma_3^2 & \mathbf{I}\sigma \\ & \mathbf{A}\sigma_1^2 & \mathbf{A}\sigma_{12} & 0 & 0\\ & & \mathbf{A}\sigma_2^2 & 0 & 0\\ & & & \mathbf{I}\sigma_3^2 & 0\\ & & & & \mathbf{I}\sigma \end{bmatrix}$$

where:

$$\mathbf{V} = \mathbf{Z}_1\mathbf{A}\mathbf{Z}_1'\sigma_1^2 + (\mathbf{Z}_1\mathbf{A}\mathbf{Z}_2' + \mathbf{Z}_2\mathbf{A}\mathbf{Z}_1')\sigma_{12} + \mathbf{Z}_2\mathbf{A}\mathbf{Z}_2'\sigma_2^2 + \mathbf{Z}_3\mathbf{Z}_3'\sigma_3^2 + \mathbf{I}\sigma_e^2$$

σ_1^2, σ_2^2, σ_3^2 and σ_e^2 = variances of sires, MGS, dam within MGS and residual effects, respectively;

σ_{12} = covariance between sire and MGS effects;

$\mathbf{A}$ = numerator relationship matrix among bulls which included both sires and MGS. In total, 10 348 pedigree bulls over 5 generations were generated from 9 400 bulls represented in the data. The relationships between dams were ignored.

The corresponding mixed model equations after absorption of fixed effects were:

$$\begin{bmatrix} \mathbf{Z}_1'\mathbf{M}\mathbf{Z}_1+\mathbf{A}^{-1}k^{11} & \mathbf{Z}_1'\mathbf{M}\mathbf{Z}_2+\mathbf{A}^{-1}k^{12} & \mathbf{Z}_1'\mathbf{M}\mathbf{Z}_3 \\ \mathbf{Z}_2'\mathbf{M}\mathbf{Z}_1+\mathbf{A}^{-1}k^{12} & \mathbf{Z}_2'\mathbf{M}\mathbf{Z}_2+\mathbf{A}^{-1}k^{22} & \mathbf{Z}_2'\mathbf{M}\mathbf{Z}_3 \\ \mathbf{Z}_3'\mathbf{M}\mathbf{Z}_1 & \mathbf{Z}_3'\mathbf{M}\mathbf{Z}_2 & \mathbf{Z}_3'\mathbf{M}\mathbf{Z}_3+\mathbf{I}k^{33} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{u}}_1 \\ \hat{\mathbf{u}}_2 \\ \hat{\mathbf{u}}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{Z}_1'\mathbf{M}\mathbf{y} \\ \mathbf{Z}_2'\mathbf{M}\mathbf{y} \\ \mathbf{Z}_3'\mathbf{M}\mathbf{y} \end{bmatrix} \quad [1]$$

where:

$$\mathbf{M}=\mathbf{I}-\mathbf{X}(\mathbf{X}'\mathbf{X})^{-}\mathbf{X}';$$

$$\begin{bmatrix} k^{11} & k^{12} & 0 \\ k^{12} & k^{22} & 0 \\ 0 & 0 & k^{33} \end{bmatrix} = \begin{bmatrix} \sigma_1^2 & \sigma_{12} & 0 \\ \sigma_{12} & \sigma_2^2 & 0 \\ 0 & 0 & \sigma_3^2 \end{bmatrix}^{-1} \times \sigma_e^2$$

The tilde-hat approach of Van Raden and Jung (1988) involves quadratics which are functions of solutions and approximate solutions for the random effects of the mixed model equations [1]. The approximate solutions were obtained by (Bertrand and Benyshek, 1987):

$$\begin{bmatrix} \tilde{\mathbf{u}}_1 \\ \tilde{\mathbf{u}}_2 \\ \tilde{\mathbf{u}}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{D}_{11} & \mathbf{D}_{12} & 0 \\ \mathbf{D}_{12} & \mathbf{D}_{22} & 0 \\ 0 & 0 & \mathbf{D}_{33} \end{bmatrix}^{-1} \begin{bmatrix} \mathbf{Z}_1'\mathbf{M}\mathbf{y} \\ \mathbf{Z}_2'\mathbf{M}\mathbf{y} \\ \mathbf{Z}_3'\mathbf{M}\mathbf{y} \end{bmatrix} = \begin{bmatrix} \mathbf{D}^{11} & \mathbf{D}^{12} & 0 \\ \mathbf{D}^{12} & \mathbf{D}^{22} & 0 \\ 0 & 0 & \mathbf{D}^{33} \end{bmatrix} \begin{bmatrix} \mathbf{Z}_1'\mathbf{M}\mathbf{y} \\ \mathbf{Z}_2'\mathbf{M}\mathbf{y} \\ \mathbf{Z}_3'\mathbf{M}\mathbf{y} \end{bmatrix}$$

where $\mathbf{D}_{11}$, $\mathbf{D}_{12}$, $\mathbf{D}_{22}$ and $\mathbf{D}_{33}$ are diagonal matrices with diagonal elements identical to those of the matrices $\mathbf{Z}_1'\mathbf{M}\mathbf{Z}_1+\mathbf{A}^{-1}k^{11}$, $\mathbf{Z}_1'\mathbf{M}\mathbf{Z}_2+\mathbf{A}^{-1}k^{12}$, $\mathbf{Z}_2'\mathbf{M}\mathbf{Z}_2+\mathbf{A}^{-1}k^{22}$ and $\mathbf{Z}_3'\mathbf{M}\mathbf{Z}_3+\mathbf{I}k^{33}$, respectively.

In fact, the diagonals of matrix $\mathbf{Z}_1'\mathbf{Z}_2$ were zero due to removal of calves having the same bull as sire and MGS. However, those of $\mathbf{Z}_1'\mathbf{M}\mathbf{Z}_2(\mathbf{Z}_1'\mathbf{Z}_2$ after absorption of fixed effects) were not equal to zero.

The general formula for a model with p possibly correlated random effects is:

$$\mathbf{E}(\hat{\mathbf{u}}_i'\mathbf{A}^{-1}\tilde{\mathbf{u}}_j)=\mathbf{tr}\left(\sum_{h=1}^{p}\sum_{k=1}^{p}\mathbf{D}^{jk}\mathbf{Z}_k'\mathbf{M}\mathbf{Z}_h\sigma_{ih}\right)$$

where: i, j, h and $k=1,2,\ldots,p$, *ie* the number of random effects in the model.

For the model assumed in this study, 5 quadratics ($\hat{\mathbf{u}}_1'\mathbf{A}^{-1}\tilde{\mathbf{u}}_1'$, $\hat{\mathbf{u}}_1'\mathbf{A}^{-1}\tilde{\mathbf{u}}_2$, $\hat{\mathbf{u}}_2'\mathbf{A}^{-1}\tilde{\mathbf{u}}_1$, $\hat{\mathbf{u}}_2'\mathbf{A}^{-1}\tilde{\mathbf{u}}_2$ and $\hat{\mathbf{u}}_3'\tilde{\mathbf{u}}_3$) were used to estimate 4 (co)variance components (σ_1^2, σ_{12}, σ_2^2, and σ_3^2). As more quadratics were available than unknown variance components the least squares approach was used.

The residual variance (σ_e^2) was estimated by the following formula:

$$\hat{\sigma}_e^2=(\mathbf{y}'\mathbf{M}\mathbf{y}-\hat{\mathbf{u}}_1'\mathbf{Z}_1'\mathbf{M}\mathbf{y}-\hat{\mathbf{u}}_2'\mathbf{Z}_2'\mathbf{M}\mathbf{y}-\hat{\mathbf{u}}_3'\mathbf{Z}_3'\mathbf{M}\mathbf{y})/(N-r(\mathbf{X})).$$

where:

N = total number of observations in the analyses;

$r(\mathbf{X})$ = rank of matrix $\mathbf{X}$.

The tilde-hat procedure requires only the diagonals of the coefficient matrix in equations [1] for (co)variance estimation. Consequently, the mixed model equations were not explicitly constructed, and solutions for random effects in equations [1] were obtained by the direct iteration approach on data (Schaeffer and Kennedy, 1986; Mandredi, 1990; Mandredi *et al*, 1991). Thus, 2 levels of nested iterations were involved for the analyses. Solutions for fixed and random effects were first obtained from the inner iterations. After 15 iterations or when the convergence criterion attained 10^{-7}, the outer iteration was then implemented for the estimation of the variance components. Iteration was finally stopped after a value of 10^{-7} for convergence was reached. The criterion of convergence (θ) was calculated as follows:

$$\theta = \sqrt{\sum_{i=1}^{n}(\phi_i^{(k+1)} - \phi_i^k)^2 / \sum_{i=1}^{n}(\phi_i^{(k+1)})^2}$$

where:

ϕ_i = solutions for fixed and random effects for the inner iteration, and variance components for the outer interation;

k = number of iterations;

n = total levels for fixed and random effects in the inner iteration, and is 5 for the outer iteration.

The expectations of the (co)variances estimated from model [1] were as follows:

$$\begin{aligned}
E(\sigma_1^2) &= (1/4)\sigma_A^2;\\
E(\sigma_2^2) &= (1/16)\sigma_A^2 + (1/4)\sigma_{AM} + (1/4)\sigma_M^2;\\
E(\sigma_3^2) &= (3/16)\sigma_A^2 + (3/4)\sigma_{AM} + (3/4)\sigma_M^2 + \sigma_C^2;\\
E(\sigma_e^2) &= (1/2)\sigma_A^2 + \sigma_E^2;\\
E(\sigma_{12}) &= (1/8)\sigma_A^2 + (1/4)\sigma_{AM};
\end{aligned}$$

where:

σ_A^2 and σ_M^2 = genetic variances of direct and maternal effects, respectively;

σ_{AM} = covariance between direct and maternal genetic effects;

σ_C^2 = variance of maternal permanent environmental effects;

σ_E^2 = variance of environmental effects.

The genetic and environmental parameters were estimated as:

$$\begin{aligned}
\sigma^2 &= \sigma_A^2 + \sigma_{AM} + \sigma_M^2 + \sigma_C^2 + \sigma_E^2;\\
h_A^2 &= \sigma_A^2/\sigma^2;\\
h_M^2 &= \sigma_M^2/\sigma^2;\\
c^2 &= \sigma_C^2/\sigma^2;\\
h_T^2 &= (\sigma_A^2 + 1.5\sigma_{AM} + 0.5\sigma_M^2)/\sigma^2;\\
r_{AM} &= \sigma_{AM}/\sigma_A\sigma_M;\\
r_{SMGS} &= \sigma_{12}/\sigma_1\sigma_2;
\end{aligned}$$

where σ^2 is the total phenotypic variance, h_A^2 is the direct heritability, h_M^2 is the maternal heritability and h_T^2 is the total heritability as defined by Dickerson (1947), c^2 is the proportion of phenotypic variance imputable to the maternal permanent environmental effects, r_{AM} is the correlation between direct and maternal additive genetics effects, r_{SMGS} is the correlation between sire and maternal grandsire effects.

RESULTS AND DISCUSSION

Table III and table IV show estimates of (co)variances and estimates of heritabilities and correlations, respectively.

Table III. Variance and covariance estimates [a] for preweaning growth and conformation at weaning in French Limousin breed.

Traits	*Sire*	*MGS*	*Cov*	*Dam*	*Res*
Weights (kg):					
Birth weight	0.53	0.16	0.16	0.79	5.3
120-d weight	15.1	10.1	4.7	47.3	158.9
210-d weight	34.1	19.6	11.2	102.1	361.8
Average daily gains (g/d):					
G_{0-120}	883	637	275	3 018	10 520
$G_{120-210}$	968	269	227	1 729	14 401
G_{0-210}	697	412	222	2 192	7 898
Conformation (total score / 100):					
Muscular development	3.67	0.98	1.16	4.28	36.91
Skeletal development	2.43	0.69	0.78	3.46	24.46

[a] Sire, MGS, Dam, and Res represent sire, maternal grandsire, dam, and residual effects, respectively. Cov is the covariance between sire and MGS effects.

Table IV. Estimates of genetic parameters for preweaning growth and conformation at weaning in French Limousin breed.

Traits	*Heritability*				*Correlation*	
	a h^2_A	a h^2_M	a h^2_T	b c^2	c r_{SMGS}	c r_{AM}
Weights:						
Birth weight	0.31	0.08	0.26	0.05	0.55	−0.40
120-d weight	0.26	0.16	0.27	0.07	0.38	−0.24
210-d weight	0.26	0.13	0.26	0.08	0.43	−0.24
Average daily gains:						
G_{0-120}	0.23	0.15	0.25	0.07	0.37	−0.23
$G_{120-210}$	0.22	0.07	0.17	0.05	0.44	−0.49
G_{0-210}	0.25	0.13	0.25	0.09	0.41	−0.25
Conformation:						
Muscular development	0.32	0.06	0.26	0.03	0.61	−0.41
Skeletal development	0.31	0.07	0.26	0.04	0.60	−0.38

[a] A, M and T represent direct and maternal genetic effects and total heritable genetic effects, respectively; [b] c^2 is the ratio of maternal permanent environmental variance to the total phenotypic variance; [c] r_{SMGS} and r_{AM} are correlations between sire and MGS, and between direct and maternal genetic effects, respectively.

Direct and maternal parameters for preweaning growth traits

Estimates of direct heritabilities of birth and weaning weights and preweaning gain from birth to weaning (h^2_A = 0.31, 0.26 and 0.25, respectively) were in close agreement with the median values of literature surveys (Petty and Cartwright, 1966; Baker, 1980; Meyer, 1992; Renand *et al*, 1992) but higher than values reported in the North American Limousin breed (0.22 and 0.16 for birth and weaning weights, respectively; Bertrand and Benyshek, 1987).

Maternal heritability estimates in this study were lower than direct heritabilities of the corresponding traits (h^2_M = 0.08, 0.13 and 0.13, respectively). Most literature estimates for maternal genetic heritability ranged from 0.05 to 0.25 for birth weight, and 0.10 to 0.35 for preweaning gain or weaning weight (Quaas *et al*, 1985; Bertrand and Benyshek, 1987; Wright *et al*, 1987; Trus and Wilton, 1988; Garrick *et al*, 1989; Kriese *et al*, 1991; Ménissier and Frisch, 1992; Meyer, 1992). The present estimates for maternal genetic effects in French Limousin breed were in the lower tail of the ranges.

The estimates of the ratio between the maternal permanent environmental variances and the phenotypic variances were small in the French Limousin breed, ranging from 0.05 to 0.09. These values were in accordance with the reports given by Bertrand and Benyshek (1987), Wright *et al* (1987) and Meyer (1992).

Correlation estimates between direct and maternal genetic effects were found to be negative in this study (table IV) and in accordance with the estimates in the

North American Limousin breed ($r_{AM} = -0.16$ and -0.30 for birth and weaning weights, respectively; Bertrand and Benyshek, 1987). Moreover, the majority of reports in the literature indicated negative r_{AM} of similar traits (Ménissier, 1976; Quaas *et al*, 1985; Bertrand and Benyshek, 1987; Cantet *et al*, 1988; Trus and Wilton, 1988; Garrick *et al*, 1989; Kriese *et al*, 1991; Ménissier and Frisch, 1992; Meyer, 1992). These estimates frequently ranged from 0 to −0.5 However, some positive direct-maternal genetic correlations were also reported (Wright *et al*, 1987; Northcutt *et al*, 1991; Trus and Wilton, 1988; Meyer, 1992).

As a matter of fact, considerable variation exists in the literature estimates of direct and maternal effects and their covariance components. This can be attributed to a number of factors, *eg* methods of estimation, statistical models, data resources (experimental or field data, breeds and production systems), assortive matings or previous selection. On the other hand, even with the most realistic model, the maternal animal model, some effects were always assumed to be absent due to computational limitation. For instance, a covariance between maternal and direct environments may exist (resulting from side effects of high nutrition during rearing of heifers on their milk ability; Mangus and Brinks, 1971) and consequently may bias the estimation of covariance between direct and maternal genetic effects (Koch, 1972; Baker, 1980; Willham, 1980; Canter *et al*, 1988). Otherwise, relatively large sampling variances of the estimates could exist for maternally influenced traits (Thompson, 1976; Foulley and Lefort, 1978; Cantet, 1990; Meyer, 1992).

Weaning weights of beef calves depend primarily upon the joint expression of preweaning growth potential of calves and maternal traits (primarily the milk production) of their dams. The relative importance of direct and maternal effects on growth may be better expressed by the estimates for preweaning growth rate (G_{0-120}, $G_{120-210}$ or 120-d weight. The estimates for both direct and maternal effects of 120-d weight were very similar to those of 210-d weight, with maternal effects being slightly more important for 120-d weight (table IV). This is realistic since calves are able to eat supplemental feed at the later stage of lactation. As shown by Neville (1962) and Le Neindre *et al* (1976), milk production was more important during the early period of the calf's life, and declined slightly up to weaning. A much lower direct heritability was obtained using a dam–offspring relationship by Molinuevo and Vissac (1972) in the same breed. This confirms the negative relationship between direct and maternal effects. The estimates for G_{0-120} were very similar to those of 120-d weight for both heritabilities for, and correlation between direct and maternal effects. For the growth period from 120 d to 210 d, however, the maternal genetic variation had been greatly reduced compared to the earlier period of growth (table III) and consequently maternal heritability was lower ($h^2_M = 0.07$) than for G_{0-120} ($h^2_M = 0.15$). It was the only trait with different (lower) total heritability (table IV). The maternal influence of 210-d weight was apparently a carry-over effect. Rutledge *et al* (1971) reported that when measures of milk yield for the first 4 months were in the model, inclusion of measures from the remaining 3 months did not lead to a significant reduction in the residual sum of squares. Further, the antagonism between direct and maternal effects was stronger in the later period of growth (table IV). This fact might be induced by more pronounced interaction between environmental factors (maternal, calf feed supplies) and calf growth compensation, for which interaction might contribute to the inflated negative covariance between maternal and direct environments that is always assumed to be zero in models. As suggested by Robison (1981), calves from dams producing less milk are forced to seek supplemental feed earlier which may over-compensate for the extra milk production by other dams. Such over-compensation is as important as the calf becomes older and concentrate is supplied. Moreover, especially for the growth period of 120-d to 210-d, the estimated ratio between maternal permanent environmental variances and phenotypic variances was small (table IV).

Direct and maternal parameters for conformation at weaning

The results of this study showed that MD and SD were moderately heritable and mainly controlled by direct genetic effects rather than maternal genetic effects (table IV). The present direct heritabilities of MD and SD were similar to the estimates of Laloë *et al* (1988) in French Limousin cattle. For overall conformation score at weaning, Petty and Cartwright (1966) reported an average value of 0.36 of direct genetic heritability from 24 estimates. The same value was obtained by Vesely and Robison (1971) for Hereford cattle.

Due to the antagonism between direct and maternal genetic effects, the total heritabilities for both MD and SD were slightly reduced. Moderate heritabilities indicate that direct selection for conformation at weaning should be efficient. However, a small negative response of the maternal ability will result. Muscularity is desirable for carcass quality. However, improved muscularity may lead to a deterioration of maternal calving ability due to the late maturing rate of the pelvic opening (Ménissier and Frisch, 1992).

The estimates of the ratio between the maternal permanent environmental variances and the phenotypic variances were smaller for both conformation traits (0.03 to 0.04) than for weights or preweaning gain.

CONCLUSION

The preweaning growth genetic parameters in this study show that the growth genetic variability is different for different growth stages. Foetal growth, measured by birth weight, is largely influenced by direct genetic effects, with an important foeto-maternal regulation as shown by a negative genetic correlation between direct and maternal effects. Otherwise, maternal effects are more important for early growth after birth, with a still negative but lower genetic correlation between direct and maternal effects. Close to weaning, maternal influences are smaller for growth, and, similarly, beef conformation at weaning is largely controlled by direct genetic effects.

From a selection point of view, weaning weight or growth to weaning is heritable enough to allow an efficient selection for direct genetic effects, *ie* for the calf's growth ability. However, selection solely for direct genetic effects does not lead to improvement of the cow's maternal ability, and could even result in deterioration of the maternal ability because of the negative correlation between maternal and direct genetic effects. Selection for combination of direct and maternal effects is necessary for the genetic improvement of beef cattle used both as sire and pure breeds such as the French Limousin cattle. The maternal genetic parameters of the different preweaning growth stages show that, among the analysed traits, 120 d weight or growth from birth to 120 d is a good selection criterion for carrying out a joint selection on cows' suckling ability (maternal effects) and calve's growth capacity (direct effects).

On the other hand, it is essential to have estimates of genetic correlations between traits for both maternal and direct effects, in order to optimize the choice of measurements and selection criteria for preweaning growth.

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