

Expected efficiency of selection for growth in a French beef cattle breeding scheme. I. Multistage selection of bulls used in artificial insemination

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Summary – Genetic improvement of beef cattle for growth traits implies selection on both direct and maternal effects through on-farm and station individual and progeny performance tests. To optimize the use of these tools, a French selection scheme of artificial insemination (AI) bulls is modelled, including its main components, *ie* 2 kinds of station performance tests and 2 kinds of progeny tests (farm and station). Three breeding objectives are derived in order to represent the heterogeneity of production systems: *Hs* for suckler herds, *Hf* for suckler-fattening herds and an average objective *Hg* considered as the most realistic for the whole breed. These objectives include direct and maternal genetic effects on weaning weight and direct effects on final weight. Economic, demographic and genetic parameters are derived for the Limousin breed. Multistage selection procedures are algebraically optimized by finding selection thresholds which maximize response for the breeding objectives. The current scheme appears to be more efficient for *Hf* than for *Hs*. However, whatever the objective, maternal genetic response is expected to be slightly negative, due to a negative correlation between direct and maternal genetic effects. Standard deviations of genetic responses are calculated to take into account some uncertainty on estimates of genetic parameters. With a 95% confidence interval, maternal genetic response could be positive. An alternative to this complex scheme is considered, using only one kind of station performance test and the on-farm progeny test. The increase of on-farm progeny test capacity reduces the value of station progeny test for selecting AI bulls, at least when only direct and maternal effects on growth traits are considered. For the simplified scheme, maternal response is expected to be positive, though uncertain due to a large standard deviation.

beef cattle / breeding objective / growth / maternal effects / sampling variance

Résumé – Prédiction de l'efficacité d'un schéma de sélection français sur la croissance en race bovine allaitante. I. Sélection par étapes des taureaux destinés à l'insémination artificielle. *En races bovines allaitantes, l'amélioration génétique des caractères de croissance passe par la sélection des effets directs et des effets maternels par contrôles individuel et de descendance, en ferme et en station. Pour optimiser l'emploi de ces outils, un schéma de sélection français des taureaux d'IA a été modélisé en considérant ses principales complexités : 2 types de stations de contrôle individuel et 2 types de contrôles de descendance (en ferme et en station). Afin de prendre en compte l'hétérogénéité des systèmes de production, 3 objectifs de sélection ont été établis : Hs pour les élevages naisseurs, Hf pour les élevages naisseurs-engraisseurs et un objectif moyen Hg, considéré comme le plus réaliste pour l'ensemble des troupeaux de la race. Ces objectifs comportent les effets directs et maternels sur le poids au sevrage ainsi que les effets directs sur le poids final d'engraissement. Les paramètres économiques, démographiques et génétiques utilisés correspondent à la situation de la race Limousine. La sélection à plusieurs étapes est optimisée algébriquement en calculant les seuils de troncature qui maximisent la réponse sur l'objectif de sélection. Le schéma de sélection semble plus efficace pour un objectif naisseur-engraisseur que pour un objectif naisseur. Toutefois, quel que soit l'objectif, la réponse sur les effets maternels est légèrement négative en raison de l'antagonisme génétique entre effets directs et maternels. L'incertitude sur les estimées des paramètres génétiques est prise en compte en calculant les écarts types de réponses à la sélection. Si l'on considère l'intervalle de confiance à 95%, une réponse positive pourrait être obtenue sur les effets maternels. Un schéma simplifié a été étudié, n'utilisant qu'un seul type de station de contrôle individuel ainsi que le seul contrôle sur descendance en ferme. Dans une perspective d'accroissement de la capacité d'évaluation sur descendance en ferme, il apparaît qu'une sélection de taureaux d'IA sur descendance en station perd de son intérêt technique, du moins quand seuls les effets directs et maternels sur la croissance sont considérés. En schéma simplifié, une réponse positive est espérée sur les effets maternels, mais n'est pas assurée, en raison de l'importance de l'écart type de la réponse.*

bovin allaitant / objectif de sélection / croissance / effets maternels / variance d'échantillonnage

INTRODUCTION

Beef cattle breeding in France takes 2 kinds of traits into account (Ménissier and Frisch, 1992): beef traits (growth, morphology, feed efficiency, carcass quality) and maternal performance (fertility, ease of calving, mothering ability). From a national viewpoint, the relative economic importance of these traits depends on the relative proportion of suckler herds and suckler-fattening herds. In a suckler herd, calves are sold at weaning (around 7–8 months) to be partly fattened outside France, in a suckler-fattening herd, calves are reared to slaughter at around 14–18 months. Over the last 10 years, the decrease of industrial crossing and the need for reducing production costs and labor requirements have led to more emphasis being placed on beef cow productivity (Ménissier, 1988). This has led to the introduction of specific evaluation procedures for maternal performance into French beef cattle breeding schemes (Ménissier *et al*, 1982).

Modelling and optimization of these breeding schemes imply taking into account several points that are unusual in dairy cattle schemes: multistage selection with

independent culling levels on highly correlated traits; the heterogeneity of genetic levels among newborn candidates for selection due to the joint use of natural service (NS) and artificial insemination (AI) bulls; and the large uncertainty in estimates of certain genetic parameters, especially concerning correlations between direct and maternal effects.

The purpose of this paper is to analyze the predicted efficiency of the current AI bull selection scheme for growth, when maternal effects are considered. This is an extension of previous work (Colleau and Elsen, 1988) which considered only selection on direct effects for final weight. The study uses the parameters and the scheme organisation of the Limousin breed, taken as a representative example of French beef cattle breeding schemes.

Three major questions are investigated in this first paper. 1) How can the AI bull multistage selection in the current breeding scheme be optimized? 2) Given the accuracies and sampling correlations of the estimated genetic parameters, what is the accuracy of predicted responses? 3) Should alternative breeding schemes be envisaged for AI bull selection? The objective of the next paper in this issue (Phocas *et al.*, 1995) is to take into account both reproduction methods (AI and NS) and female selection paths. For both papers, theoretical problems of general interest are investigated. How can we calculate the accuracy of predicted responses? How can we calculate asymptotic genetic gains in heterogeneous populations?

MATERIALS AND METHODS

The meanings of abbreviations used in the text and tables are given in *Appendix I*.

Deriving a relevant breeding objective

The economic values of beef cattle production traits differ according to production systems and circumstantial parameters, as recalled by Doren *et al.* (1985). Hence, the derivation of the selection objective should account for the existence of 2 main kinds of production herds, depending on how progeny are sold: at weaning in a suckler herd; and after fattening in a suckler-fattening herd. Calves were assumed to be sold at a constant age: 210 d at weaning (67%) or 500 d after fattening (33%). Only growth was considered in the present study. In order to distinguish the genetic influence of dam's suckling ability on calf growth from her genetic direct transmitting ability, a suckler herd breeding objective (H_s) was derived, which includes maternal effects (M210) on weaning weight (W210) together with direct effects (A210). For suckler-fattening herds, the breeding objective (H_f) also took into account direct (A500) on final weight (W500). A combined objective (H_g) was built from H_s and H_f to represent the true economic objective of the breed. The economic weights of H_g were derived from the relative proportion of calves sold at weaning (2:3) compared to calves sold at 500 d (1:3): $H_g = 2/3 H_s + 1/3 H_f$.

In order to maximize the profit for trait i per animal sold, the partial derivative of profit with respect to a unit change in that trait was computed. This is called the economic margin (a_i) for trait i . Direct and maternal expression of the same trait were considered as 2 different traits j and k . Figures used for derivation of economic margins are presented in table I. Prices, average weights and feed

costs differ according to sex. Thus, economic margins were computed for each sex and average values were derived by weighting values for each sex by the relative frequency of males (or females) sold. The prices used were those indicated by Belard *et al* (1992). Relative economic margins are basically dependent on assumptions about feeding diets. Direct effects on preweaning growth are less profitable than maternal effects, because an additional kilogram of weaning weight due to direct effects was obtained from concentrate, which is an expensive feed source compared to milk. Growth from maternal milk is more valuable because dams partly produce milk from forage and pasture, *ie* a cheap feed source. Likewise, economic margin per additional kilogram of final weight was higher than before weaning, because cheaper feed sources, such as maize silage, are used. *Appendix II* presents a full description of the calculation.

Table I. Figures used for derivation of economic margins.

<i>Criterion</i>	<i>Male</i>	<i>Female</i>
Average live weight (kg)		
At 210 d	300	275
At 500 d	600	475
Sex ratio for calves sold (%)		
At 210 d	73	27
At 500 d	55	45
Price per kg sold in 1991 (FF)		
At 210 d	17.2	15.7
At 500 d	15.5	17.5
Marginal feed cost per kg (FF)		
At 210 d		
<i>Maternal effect</i>	3.0	3.0
<i>Direct effect</i>	6.5	6.5
At 500 d		
<i>Direct effect</i>	6.1	3.5

FF: French francs.

The following breeding objectives (in FF) were derived, with As and Ms in kilograms:

- the suckler objective: $H_s = 10 A_{210} + 14 M_{210}$
- the suckler-fattening objective: $H_f = -5 A_{210} - 1 M_{210} + 12 A_{500}$
- the global objective: $H_g = 5 A_{210} + 9 M_{210} + 4 A_{500}$

In the past, some theoretical studies (Hanrahan, 1976; Van Vleck *et al*, 1977; Hanset, 1981; Azzam and Nielsen, 1987) presented breeding objectives with the same economic weight for direct and maternal effects, without any justification of this choice. As far as we know, only Ponzoni and Newman (1989) separated direct and maternal effects in the breeding objective for Australian beef cattle. However, they assumed that 1 kg of W210 due to direct effects has the same cost as 1 kg of W210 due to maternal effects. The only difference they considered was the number of expressions of direct effects compared to the number of expressions of maternal

effects within a 20-year period and for a 5% discount rate. However, the ratio of numbers of direct expressions to maternal ones depends very much on the discount rate and, to a lesser extent, on the assumptions concerning the population structure. For a zero discount rate and overlapping generations, this ratio is asymptotically equal to 1 for any population structure without a closed nucleus. Since our purpose was to calculate asymptotic genetic gains (Phocas *et al*, 1995), we found that it was more consistent to derive the breeding objective from the asymptotic ratio of expressions, *ie* for the same number of direct and maternal expressions.

Description of the breeding scheme

The Limousin breed is the second French beef cattle breed with about 600 000 cows; 10% of these cows are registered and recorded, and they constitute the selection nucleus. The AI rate is about 10% in the nucleus and about 20% in the whole Limousin population. The current selection program has been implemented since 1980 and combines both AI and NS bull selection. Selection is performed in a sequential way with independent culling levels on individual and progeny performance. Complexity is induced by the existence of 2 paths for AI bull selection. Each of these paths implies an individual station performance test and a progeny performance test (fig 1). In the first path, AI bulls are selected after a 'long performance test' and a progeny test in station (Ménissier, 1988). Bulls are measured over 6 months on individual growth, muscular and skeletal development and feed intake; the progeny test concerns beef traits (on young bulls' production) and maternal performance (on primiparous daughters). More recently, some AI bulls have completed tests from a cheaper selection program, which reduced costs for individual performance testing (a 4-month period without feed intake recording) and for progeny testing (on-farm, limited to direct effects on preweaning performance). This last test is performed by using reference AI bulls (the so-called 'connection sires') that provide statistical links for breeding value estimation (Foulley and Sapa, 1982). Exchange between both selection paths is currently developing.

Alternative breeding schemes might be envisaged to simplify the breeding scheme and to reduce costs. For that purpose, a simplified scheme was constructed, considering only 'short performance test' in station and progeny performance test on-farm (fig 2). The on-farm progeny index was modified to take maternal performance into account: a combined index of the average W210 of 30 sons and the average W120 of calves of bulls' daughters was built. It was assumed that heritability of maternal effects is lower on-farm ($h^2 = 0.16$) than in station ($h^2 = 0.26$), since environmental effects are better controlled in station.

Derivation and optimization of selection differentials

Optimization of selection differentials for the current breeding scheme

The AI bull selection is optimized by considering each section of the current breeding scheme as a variate within an overall multivariate selection. This leads to the use of a method previously developed by Ducrocq and Colleau (1989) for finding optimum selection thresholds in multistage selection, assuming a multivariate

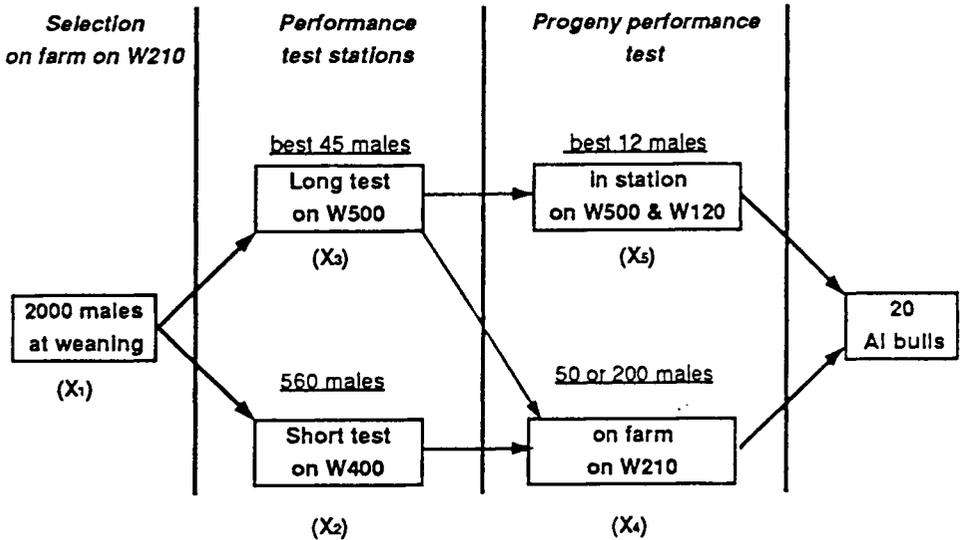


Fig 1. Current selection scheme of AI bulls.

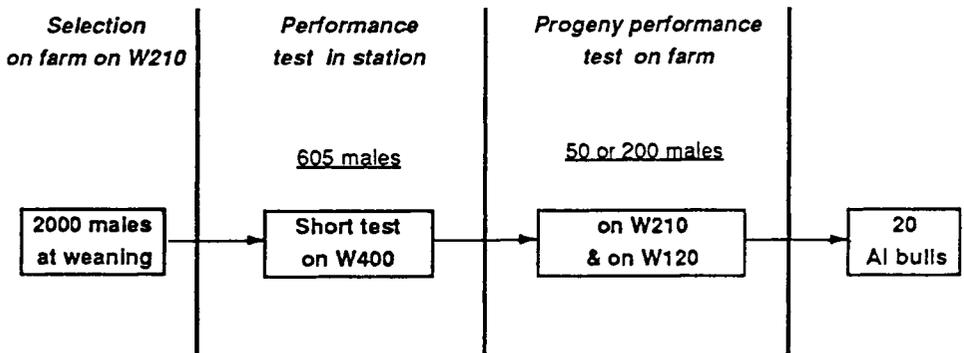


Fig 2. Simplified selection scheme of AI bulls.

normal distribution and treating candidates for selection as independent observations. Optimum selection thresholds are thresholds which maximize the selection response.

Let us define the following variables:

X_1 , the 210 d weight (W210)

X_2 , the 400 d weight (W400)

X_3 , the 500 d weight (W500)

X_4 , the average W210 of 30 sons

X_5 , the index (I_s) combining the average W500 of 30 sons and the average W120 (120 d weight) of 20 daughter's calves (1 calf per daughter).

X_1, X_2, X_3, X_4, X_5 , the breeding value H and components of H are random variables with a multivariate normal distribution. The function to maximize is the average breeding value (H) of the bulls finally selected for use in AI, whatever the origin:

$$\begin{aligned} H = & P(X_1 > a_1, X_3 > a_3, X_5 > a_5) E(H|X_1 > a_1, X_3 > a_3, X_5 > a_5) \\ & + P(X_1 > a_1, b_3 < X_3 < a_3, X_4 > a_4) E(H|X_1 > a_1, b_3 < X_3 < a_3, X_4 > a_4) \\ & + P(b_1 < X_1 < a_1, X_2 > a_2, X_4 > a_4) E(H|b_1 < X_1 < a_1, X_2 > a_2, X_4 > a_4) \end{aligned}$$

where the a_i s and the b_i s are the selection thresholds on the X_i variates.

To illustrate the reasoning, let us consider the category of on-farm progeny tested bulls selected from the 'short performance test'. These bulls are not the best ones at weaning; their weight W210 is lower than a first threshold a_1 but larger than a second threshold b_1 ($b_1 < X_1 < a_1$). A second threshold occurs on W400; the males selected for on-farm progeny test are above a threshold a_2 ($X_2 > a_2$). A final threshold a_4 has to be added as the result of on-farm progeny test selection ($X_4 > a_4$).

Thresholds a_1 and b_1 for W210 are obtained directly (fig 1). The other thresholds are computed after optimizing the above non-linear function, with constraints on the proportion of males selected for station progeny test (12:2 000), the proportion selected for on-farm progeny test (current 50:2 000 or envisaged 200:2 000) and the final proportion of AI bulls selected (20:2 000). A Newton-Raphson algorithm is set up taking these constraints into account through Lagrange multipliers.

Derivation of selection differentials for the simplified breeding scheme

For the simplified scheme, each threshold was obtained directly, since the number of candidates for each test is fixed (fig 2). Thus, there is no optimization.

Genetic parameters

Estimation

The genetic parameters used in the present study (table II) for direct and maternal effects on weight at 120 and 210 d were estimated by Shi *et al* (1993) for the French Limousin breed. The other parameters are literature averages (Renand *et al*, 1992). Correlations between selection goals and selection indices are also presented in table III. The procedure proposed by Foulley and Ollivier (1986) was used to test the consistency of phenotypic and genetic covariance matrices.

Uncertainty

As underlined by Meyer (1992), sampling covariances of estimates of variance components including maternal effects are very high even for designs specifically dedicated to the estimation of maternal effects. Thus, the accuracy of predicted responses (especially indirect responses for maternal effects) should be assessed from sampling covariances of dispersion parameters. However, these sampling covariances

Table II. Heritabilities and standard deviations^a.

<i>Trait</i>	<i>Heritability</i>	<i>Standard deviation (kg)</i>
A500	0.40	29.1
A210	0.26	11.6
M210	0.14	8.2
W210	0.26	22.8
W400	0.30	40.0
W500	0.40	46.0

^a *Appendix I* gives the meaning of the abbreviations used to designate variables.

Table III. Correlations between breeding objectives, their components, performance and progeny-test averages^a.

	<i>A500</i>	<i>A210</i>	<i>M210</i>	<i>W210</i>	<i>W400</i>	<i>W500</i>	<i>I_s</i>	<i>I_{f1}</i>	<i>I_{f2}</i>
<i>Hg</i>	0.89	0.80	0.22	0.45	0.45	0.56	0.85	0.66	0.75
<i>Hs</i>	0.50	0.62	0.61	0.42	0.28	0.31	0.77	0.51	0.81
<i>Hf</i>	0.99	0.73	-0.20	0.33	0.48	0.63	0.87	0.60	0.54
A500	1	0.80	-0.20	0.37	0.49	0.63	0.82	0.66	0.57
A210		1	-0.24	0.46	0.45	0.51	0.70	0.82	0.71
M210			1	0.06	-0.11	-0.12	0.07	-0.20	0.25
W210				1	0.75	0.70	0.37	0.38	0.41
W400					1	0.80	0.41	0.37	0.32
W500						1	0.52	0.42	0.36

^a *Appendix I* gives the meaning of abbreviations used to designate variables.

are seldom calculated because of exceedingly high computing costs. Hence, the sampling variance-covariance matrix of restricted maximum likelihood (REML) estimates for preweaning genetic parameters is derived from a theoretical layout, roughly mimicking the real structure of the data. Postweaning parameters are well known and, consequently, are not considered in this study.

The same p unrelated bulls are sires (S) of a first progeny generation and maternal grandsires (MGS) of a second progeny generation. These bulls are also unrelated to the p maternal grandsires of the first generation and the p sires of the second generation. We additionally assume that a constant number (d) of calves is obtained from each pair S-MGS and that these d offspring are born from unrelated dams. The statistical model used to analyse these data is a bivariate (W120 and W210) S-MGS model. For a c -trait model and the above layout, the sampling variance-covariance matrix of REML estimators is derived from matrices of maximal size $4c \times 4c$ (*Appendix III*). The number d of offspring per pair S-MGS is equal to 1 in our numerical application. Three numbers of bulls are considered: $p = 20, 45$ or 125; the value 45 leads to coefficients of variation on additive variances around 20%, which is a frequent value seen in literature for direct heritabilities.

θ , the vector of direct and maternal dispersion parameters, is easily obtained from θ^* , the vector of dispersion parameters of the S-MGS model: $\theta^* = \mathbf{M}\theta$ where \mathbf{M} is a constant matrix. Then $\text{Var}(\theta) = \mathbf{M}^{-1}\text{Var}(\theta^*)\mathbf{M}^{-1'}$, where $\mathbf{M}^{-1'}$ is the transposed matrix of \mathbf{M}^{-1} .

These sampling variance-covariance matrices are then used to compute the approximate variance of selection response H . H is approximated by the first-order term of a Taylor expansion. As underlined by Harris (1964), this is a common method for deriving variance of complex functions.

$$H(\theta) \approx H(\theta_0) + \mathbf{G}(\theta_0)'[\theta - \theta_0]$$

where θ_0 is the vector of unbiased point estimates ($E(\theta) = \theta_0$)

$$\text{and } \mathbf{G}(\theta_0) = \left(\frac{\partial H(\theta)}{\partial \theta} \right)_{\theta=\theta_0}$$

$$\text{Var}[H(\theta)] \approx \mathbf{G}(\theta_0)'[\text{Var}(\theta - \theta_0)]\mathbf{G}(\theta_0)$$

Obtaining the first derivatives is tedious. Thus, they are computed by finite differences of H :

$$G_i(\theta_0) = \frac{1}{e} [H(\theta_0 + 0.5\epsilon_i) - H(\theta_0 - 0.5\epsilon_i)]$$

where $G_i(\theta_0)$ is the i th term of $\mathbf{G}(\theta_0)$

and ϵ_i is a vector of zeros except the i th term which is equal to e . For e between 10^{-2} and 10^{-5} kg², the results are very stable: the first 4 decimals of the sampling standard deviation of the standardized selection differential are always the same.

RESULTS AND DISCUSSION

Efficiency of the current selection scheme

Optimum choice of AI bulls according to their origin

The optimum number of AI bulls to select after on-farm progeny test is almost independent of the objective and of the farm progeny test capacity (either 50 or 200 bulls). It varies from 13 to 14 males out of the 20 AI bulls selected (table IV). The majority of AI bulls are selected after the on-farm progeny test due to a larger progeny test capacity compared to the station progeny test capacity (12 bulls). However, the probability of selection is higher for a station progeny tested bull: more than 50% (6 or 7 bulls out of 12) *versus* less than 30% (13 or 14 bulls out of 50 or 200) for on-farm progeny tested bulls. If the objective includes final weight, the station progeny tested bulls are favored because the corresponding direct effects are better assessed in the 'long performance test'. If the objective concerns weaning weight, they are favored because they are the best at weaning (fig 1) and also because the maternal performance of their daughters is assessed.

Table IV. Origin of the 20 selected AI bulls according to breeding objective and farm progeny test capacity.

Breeding objective	No of on-farm progeny tested bulls	No of bulls selected		
		Station progeny test and long performance test	On-farm progeny test	
			Long performance test	Short performance test
Global (<i>Hg</i>)	50	7	6	7
	200	6	3	11
Suckler (<i>Hs</i>)	50	6	9	5
	200	6	3	11
Suckler-fattener (<i>Hf</i>)	50	7	3	10
	200	6	2	12

By assumption, all the AI bulls selected after station progeny test were first evaluated in a 'long performance test'. Conversely, the location of performance test of the 13 or 14 bulls selected after on-farm progeny test depends very much on breeding objective and on progeny test capacity (table IV). At low progeny test capacity, the numbers of these AI bulls first selected in the 'long performance test' are 9, 3 and 6, respectively for *Hs*, *Hf* and *Hg*; at higher progeny test capacity, the corresponding numbers are 3, 2 and 3. Therefore, different selection policies should be employed for bulls used in suckler herds or suckler-fattening herds.

Selection responses

The maximal selection responses for each of the 3 objectives studied are presented in table V. In each case, the selection response in *Hg* is given in order to evaluate the loss of efficiency occurring when the objective considered (*Hs*, *Hf*) does not correspond to the true economic objective for the breed (*Hg*).

At low progeny test capacity on-farm, selection responses range from $1.38 \sigma_{Hs}$ when selecting on *Hs* to $1.72 \sigma_{Hg}$ when selecting on *Hg*. The scheme appears to be more efficient for suckler-fattening herds than for suckler herds. However, the highest efficiency occurs when selecting for *Hg*. Whatever the objective, an improvement of direct effects is expected, but the genetic trend of maternal effects on W210 is negative (table VI). This stems basically from the genetic antagonism between direct and maternal effects ($rg = -0.24$).

Selection responses are 3–6% larger at high *versus* low farm test capacity. This increase is more significant for *Hg* than for *Hs* or *Hf*, due to the higher accuracy of on-farm progeny selection index I_{f1} (table III) for predicting *Hg* than for predicting *Hf* or *Hs*. Moreover, the impact of a higher farm progeny test capacity is less significant for *Hs* than for *Hg* or *Hf*, since farm progeny tested bulls are not evaluated on maternal performance.

Table V. Expected selection responses (in σ_H units).

<i>Breeding objective</i> H_i	<i>No of farm progeny tested bulls</i>	<i>Response in H_i</i>	<i>Response in H_g</i>
<i>Current scheme</i>			
<i>Hg: global</i>	50	1.75	1.75
	200	1.87	1.87
<i>Hs: suckler</i>	50	1.38	1.69
	200	1.42	1.85
<i>Hf: suckler-fattener</i>	50	1.72	1.73
	200	1.77	1.85
<i>Simplified scheme</i>			
<i>Hg: global</i>	50	1.70	1.70
	200	1.97	1.97
<i>Hs: suckler</i>	50	1.41	1.69
	200	1.87	1.94
<i>Hf: suckler-fattener</i>	50	1.52	1.65
	200	1.57	1.87

Table VI. Selection responses (in σ_G units) in the basic traits: expected values and standard deviation for a medium uncertainty^a in preweaning genetic parameters (in brackets).

<i>Breeding objective</i>	<i>No of farm progeny tested bulls</i>	<i>Weaning weight (direct)</i>	<i>Weaning weight (maternal)</i>	<i>Final weight (direct)</i>
<i>Current scheme</i>				
<i>Hg: global</i>	50	1.85 (0.22)	-0.26 (0.37)	1.75 (0.02)
	200	2.06 (0.25)	-0.35 (0.42)	1.87 (0.03)
<i>Hs: suckler</i>	50	1.80 (0.23)	-0.11 (0.34)	1.58 (0.04)
	200	2.03 (0.25)	-0.29 (0.40)	1.80 (0.04)
<i>Hf: suckler-fattener</i>	50	1.83 (0.22)	-0.39 (0.40)	1.81 (0.04)
	200	2.05 (0.25)	-0.42 (0.43)	1.89 (0.03)
<i>Simplified scheme</i>				
<i>Hg: global</i>	50	1.66 (0.20)	0.03 (0.30)	1.58 (0.06)
	200	1.89 (0.27)	0.34 (0.35)	1.66 (0.11)
<i>Hs: suckler</i>	50	1.59 (0.22)	0.14 (0.27)	1.53 (0.09)
	200	1.76 (0.31)	0.54 (0.32)	1.55 (0.17)
<i>Hf: suckler-fattener</i>	50	1.70 (0.20)	-0.15 (0.36)	1.61 (0.05)
	200	1.96 (0.26)	0.01 (0.42)	1.70 (0.09)

^a See table VII for $p = 45$ bulls.

Whatever the objective, selection response for H_g has been derived. From this calculation (table V), it can be concluded that selection response is robust to errors in determining breeding objectives. The loss of economic response for the whole

Limousin population (evaluated on Hg) would be negligible whatever the breeding objective: -3 and -1% when breeding objectives are Hs and Hf , respectively, at low progeny test capacity; -1% whatever the objective, at higher progeny test capacity.

Change in efficiency in a simplified selection scheme

The evolution of efficiency depends very much on the objective and on-farm progeny test capacity (table V). At low capacity of on-farm progeny test, the differences between the 2 schemes in selection responses range from -12 to $+2\%$. The lowest value is for the fattener objective (Hf), the highest for the calf producer objective (Hs). If selection concerns final weight, simplification of the scheme leads to a loss of efficiency since final weight is better assessed in the 'long performance test'. If selection concerns direct and maternal effects at weaning, it leads to a gain of efficiency since all bulls progeny tested are evaluated on W210 of their sons and on the maternal performance of their daughters. At high on-farm progeny test capacity, a large gain of efficiency occurs when selecting on Hs (32%) or Hg (5%) with the simplified scheme; the loss of efficiency when selecting on Hf is still 11%.

In the simplified scheme, positive maternal response is expected for Hs and Hg at low progeny test capacity, whatever the breeding objective at higher progeny test capacity.

Accuracy of predicted selection response

Some idea of the variance of predicted response is required to plan and justify a breeding program. Assuming that genetic parameters are really known, variability of selection response is due to genetic sampling and drift. Woolliams and Meuwissen (1993) show how sampling variance and expectation of selection response can be weighted to choose between alternative breeding schemes using utility theory. In our study, another aspect is considered, the variance of the predicted response due to inaccurate estimates of genetic parameters. The purpose is to clarify the situation for maternal genetic response.

Sampling variances and correlations

Three different levels of uncertainty in genetic parameters of W120 and W210 are studied, depending on the number of bulls evaluated as sires and maternal grandsires: 20, 45 or 125 bulls. The sampling variances and the sampling correlations between estimates of genetic components are presented in tables VII and VIII respectively. It should be noticed that the magnitude of sampling variances and correlations is nearly independent of the trait considered (W120 or W210).

For the case of 20 bulls, uncertainty (expressed as the ratio of the sampling standard deviation to the absolute value of the estimate of genetic component, called coefficient of variation) in direct (co)variances is around 40% whereas uncertainty in maternal (co)variances is around 80%. Uncertainties in direct and maternal (co)variances decrease to 20 and 30% respectively in the case of 45 bulls and to 10 and 14% in the case of 125 bulls. However the largest uncertainties concern the estimates of covariances between direct and maternal effects, around 200% for the

Table VII. Coefficients of variation (in %) of preweaning parameters^a.

P	$\sigma_{A_1}^2$	$\sigma_{M_1}^2$	$\sigma_{A_1M_1}$	$\sigma_{A_1A_2}$	$\sigma_{M_1M_2}$	$\sigma_{A_1M_2}$	$\sigma_{M_1A_2}$	$\sigma_{A_2}^2$	$\sigma_{M_2}^2$	$\sigma_{A_2M_2}$
20	39	86	190	41	81	216	246	40	79	198
45	20	32	88	21	33	99	114	20	34	91
125	10	14	41	11	14	46	53	10	15	42

^a p is the number of bulls evaluated as sires and maternal grandsires in order to estimate the genetic parameters (A: direct; M: maternal); subscript 1 concerns parameters for weight at 120 d; subscript 2 concerns parameters for weight at 210 d.

Table VIII. Sampling correlations between estimates of preweaning parameters for a medium uncertainty in sampling variances^a.

	$\sigma_{A_1}^2$	$\sigma_{M_1}^2$	$\sigma_{A_1M_1}$	$\sigma_{A_1A_2}$	$\sigma_{M_1M_2}$	$\sigma_{A_1M_2}$	$\sigma_{M_1A_2}$	$\sigma_{A_2}^2$	$\sigma_{M_2}^2$	$\sigma_{A_2M_2}$
$\sigma_{A_1}^2$	1	0.07	-0.31	0.94	0.06	-0.29	-0.29	0.80	0.04	-0.26
$\sigma_{M_1}^2$		1	-0.54	0.08	0.96	-0.53	-0.47	0.08	0.83	-0.46
$\sigma_{A_1M_1}$			1	-0.27	-0.54	0.92	0.89	-0.21	-0.48	0.81
$\sigma_{A_1A_2}$				1	0.07	-0.30	-0.29	0.94	0.06	-0.31
$\sigma_{M_1M_2}$					1	0.56	-0.54	0.07	0.95	-0.55
$\sigma_{A_1M_2}$						1	0.84	-0.28	-0.54	0.89
$\sigma_{M_1A_2}$							1	-0.25	-0.56	0.92
$\sigma_{A_2}^2$								1	0.07	-0.33
$\sigma_{M_2}^2$									1	-0.61
$\sigma_{A_2M_2}$										1

^a $p = 45$ bulls evaluated as sires and maternal grandsires in order to estimate the genetic parameters (A: direct; M: maternal); subscript 1 concerns parameters for weight at 120 d; subscript 2 concerns parameters for weight at 210 d.

case of 20 bulls, 100% for the case of 45 bulls and 50% for the case of 125 bulls. Sampling correlations do not differ very much according to the number of bulls. Whatever the number of bulls, the highest sampling correlations (in absolute values) are obtained between genetic components of the same kind (2 additive (co)variances, or 2 maternal (co)variances, or 2 direct-maternal covariances).

Within trait, our results lead to the same conclusions as those obtained from different structures of data and different genetic parameters by Meyer (1992). Sampling correlations between additive or maternal genetic variance and the direct-maternal covariances are medium (0.3–0.6). Sampling correlation between additive variance and maternal variance is smaller than previous correlations. In our study, this correlation is around 0.07; in Meyer's work the value ranged from 0.04 to 0.48, depending on the structure of data.

Standard deviation of predicted selection responses

Standard deviations of predicted selection responses are presented in table IX for the 3 sampling variance-covariance matrices defined above. These standard deviations are similar whatever the structure of the selection scheme (current or simplified), but depend very much on the breeding objective. They are high for *Hs* and almost nonexistent for *Hf*. This is easily explained by the fact that uncertainty was only considered for preweaning parameters. Sampling standard deviations of differentials for *Hs* are in the range of uncertainty in maternal variance of W210. Standard deviations for selection differentials in *Hg* are in the range of uncertainties in direct genetic variances. For the current scheme, these standard deviations are nearly independent of the progeny test capacity. For the simplified scheme, standard deviations increase when progeny test capacity increases. More males are evaluated on maternal performance and thus the uncertainty in preweaning parameters has a larger impact. The same comments can be made for the standard deviations of the objective components (table VI). Standard deviations of direct and maternal responses in W210 are in the range of the respective uncertainties in direct and maternal variances for W210. If 95% confidence intervals are considered, the following remark must be made. For the current scheme, the predicted maternal response could be positive but for the simplified scheme it could be negative.

Table IX. Standard deviations of standardized selection responses.

<i>Breeding objective</i>	<i>No of on-farm progeny tested (bulls)</i>	<i>Standard deviation for p=20^a</i>	<i>Standard deviation for p=45^a</i>	<i>Standard deviation for p=125^a</i>
<i>Current scheme</i>				
<i>Hg: global</i>	50	0.38	0.18	0.8
	200	0.42	0.20	0.9
<i>Hs: suckler</i>	50	0.66	0.31	0.15
	200	0.73	0.34	0.16
<i>Hf: suckler-fattener</i>	50	0.3	0.2	0.0
	200	0.2	0.1	0.0
<i>Simplified scheme</i>				
<i>Hg: global</i>	50	0.40	0.19	0.9
	200	0.52	0.24	0.12
<i>Hs: suckler</i>	50	0.61	0.28	0.13
	200	0.73	0.34	0.16
<i>Hf: suckler-fattener</i>	50	0.7	0.3	0.2
	200	0.14	0.7	0.3

^a *p* is the number of bulls evaluated as sire and maternal grandsire.

In animal breeding, only Tallis (1960), Harris (1964) and Sales and Hill (1976a, b) seem to have considered the influence of uncertain statistical dispersion parameters on the variance of predicted genetic gains. They found high variances of predicted efficiency of a selection index. Our study for a more complex selection suggests that

this aspect should not be overlooked when setting up breeding plans and evaluating genetic responses.

Analysis of sensitivity to direct-maternal correlations

Alternative analyses were carried out according to different values of direct-maternal correlation (r_{AM}): $r_{AM} = 0$ and $r_{AM} = -0.6$. Indeed, very variable values are observed in the literature. Table X presents corresponding selection responses for the 3 objectives and for the 2 breeding schemes considered in this study. Of course, all the selection responses are lower when r_{AM} is more negative. However only maternal response and response in H_s are very sensitive to r_{AM} value. Whatever the direct-maternal correlation (between 0 and -0.6), the choice of the most efficient breeding scheme is unchanged. The simplified scheme is really interesting (compared to the current scheme) for high progeny test capacity and objective H_s ; the gain in efficiency in H_s is higher as direct and maternal effects are opposed (42% for $r_{AM} = -0.6$ instead of 26% for $r_{AM} = 0$), because, in the simplified scheme, a larger number of bulls are evaluated on maternal performance. For the same reason, the loss in efficiency in H_f due to simplification of the breeding scheme is higher as r_{AM} becomes negative. The same comment can be made for H_g at low progeny test capacity. At higher progeny test capacity, a small loss in efficiency in H_g (-3%) is observed for very negative direct-maternal correlation ($r_{AM} = -0.6$), but otherwise a gain in efficiency in H_g is obtained by simplifying the breeding scheme.

Table X. Expected selection responses (in σ_H units) according to the value of genetic direct-maternal correlation (r_{AM}).

Breeding objective	r_{AM}	Responses at low progeny test capacity				Responses at high progeny test capacity			
		H	$A210$	$M210$	$A500$	H	$A210$	$M210$	$A500$
<i>Current scheme</i>									
H_g : global	0	1.82	1.89	0.23	1.75	1.93	2.08	0.16	1.88
	-0.6	1.69	1.81	-1.00	1.77	1.78	2.04	-1.13	1.85
H_s : suckler	0	1.56	1.86	0.34	1.63	1.61	2.06	0.21	1.83
	-0.6	1.03	1.71	-0.81	1.53	1.07	1.98	-1.04	1.77
H_f : suckler-fattener	0	1.78	1.85	0.07	1.82	1.78	2.06	0.08	1.90
	-0.6	1.72	1.81	-1.06	1.79	1.73	2.06	-1.20	1.84
<i>Simplified scheme</i>									
H_g : global	0	1.78	1.74	0.42	1.64	2.10	2.04	0.78	1.64
	-0.6	1.57	1.57	-0.62	1.51	1.73	1.72	-0.45	1.52
H_s : suckler	0	1.55	1.69	0.50	1.61	2.03	1.95	0.91	1.70
	-0.6	1.11	1.47	-0.48	1.44	1.52	1.54	-0.19	1.38
H_f : suckler-fattener	0	1.56	1.77	0.28	1.66	1.66	2.09	0.52	1.81
	-0.6	1.45	1.60	-0.76	1.54	1.45	1.78	-0.69	1.56

CONCLUSION

In this paper, only a section of the whole breeding scheme of a beef breed was considered, *ie* the multistage selection of AI bulls. The next paper will present calculations of expected genetic gains for the selection nucleus. Current French beef bull selection programs, such as the Limousin program, can provide important genetic gain for objectives concerning direct and maternal effects on growth. The scheme appears to be more efficient for a suckler-fattener's objective (H_f) than for a suckler's one (H_s). A combined objective H_g , which combines H_s and H_f , is taken as a reference for economic profit of the whole breed. Whatever the breeding objective considered to derive optimal selection thresholds, response in H_g is robust and is larger than responses in H_s and H_f . This is very satisfying from a national viewpoint. A slight negative genetic response in maternal effects is predicted, but is subject to uncertainty in preweaning genetic parameters. This is relatively disappointing since improving maternal effects will probably become more and more important. The trend towards extensification leads to an increased relative margin expected from improvement in maternal effects in comparison with improvement in direct effects.

A simplified scheme, keeping only a 'short performance test' and an on-farm progeny test with bull evaluation on maternal performance, would allow us to overcome this problem, at least if the true direct-maternal genetic correlation is not too far from its estimate (around -0.2). Moreover, it could induce an important gain in efficiency in H_s and H_g when on-farm progeny test capacity increases. Thus increasing on-farm progeny test capacity through the use of an animal model evaluation system applied to all beef recorded herds (Laloë and Ménissier, 1990) while simplifying the breeding scheme, might be considered as an efficient alternative to the current scheme.

However, a full evaluation of the efficiency of such selection schemes would require more complex models integrating feed efficiency, carcass composition, morphology and reproductive traits (such as fertility or ease of calving...). Indeed these traits are mainly evaluated in the 'long performance test' and in the station progeny test. However, as underlined by Newman *et al* (1992), our knowledge of genetic parameters is deficient in these areas. The lack of estimates is especially important for maternal performance and the relationship between direct and maternal effects (Ménissier and Frisch, 1992). Moreover, the necessity of obtaining accurate estimates of components of variance is underlined by the importance of variance in selection response due to uncertainty of genetic parameters when maternal effects have to be considered. This is essential for correctly ranking selection policies and predicting genetic gains.

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APPENDIX I. Meaning of abbreviations used in tables and figures

Selection criteria

W120: weight at 120 d

W210: weight at 210 d or weaning weight

W400: weight at 400 d

W500: weight at 500 d or final weight

I_s : optimum index combining average W500 of 30 bull's sons and average W120 of 20 calves of bull's daughters with maternal heritability of station W120 equal to 0.26.

I_{f1} : average W210 of 30 bull's sons.

I_{f2} : optimal index for H_i combining average W210 of 30 bull's sons and average W120 of 20 calves of bull's daughters with maternal heritability of on-farm W120 equal to 0.16.

Breeding values

A120: direct effects on W120

M120: maternal effects on W120

A210: direct effects on W210

M210: maternal effects on W210

A400: direct effects on W400

A500: direct effects on W500

Selection objectives

H_g : global objective

H_s : suckler objective

H_f : suckler-fattener objective

APPENDIX II. Derivation of breeding objectives

Derivation of margins for suckler herds

- The economic margin a_{f_1} for direct effects on final weight (A500) in a suckler herd is equal to 0 FF, since calves are sold at weaning.
- The economic margin a_{d_1} for direct effects on weaning weight (A210) in a suckler herd is equal to 10.3 FF per kg.

This corresponds to the difference between the price per kilogram sold at weaning (16.8 FF) and the feed cost (6.5 FF) of one additional kilogram at weaning, due to direct genetic effects. This cost is assumed to amount to 5 kg of concentrate at the price of 1.3 FF/kg. Recommendation for breeders (ITEB, 1991) is from 5 to 15 kg of concentrate per additional kilogram at weaning. The lowest value is considered in our calculations, because it seems to be the most likely choice for the breeder.

- The economic margin a_{m_1} for maternal effects on weaning weight (M210) in a suckler herd is equal to 13.8 FF per kg.

Maternal effects on W210 are supposed to be only due to dam's milk yield. Their marginal cost corresponds to the marginal cost of dam's feed intake. To get 1 kg heavier calves at weaning, dams should produce 8 kg more milk. This value corresponds to the ratio of the milk production to the gain of weight from birth to weaning in the Limousin breed. This may be an underestimate of the marginal number of kilograms of milk needed per additional kilogram over the average W210, which could be around 15 kg more milk. Estimates from 6 to 24 kg are observed in the literature (Drewry *et al.*, 1959; Neville, 1962; Jeffery *et al.*, 1971; Le Neindre *et al.*, 1976). As uncertainty in the correct value is important, the same strategy as for calculation of a_{d_1} is considered. The minimum possible value is used, *ie* 8 kg. The INRA feed recommendation (INRA, 1988) per additional kg of milk for a Limousin cow is 0.45 UFL (French energy units for cattle with low daily requirement, as lactating cow) and 0.3 UEB (French fill unit). Therefore, 3.6 UFL per additional kilogram of calf weaned are required, which corresponds to 2.4 UEB. The period from calving to weaning can be separated into 2 periods. During the first 3 months, animals are in cowsheds and cows are fed with a mixed ration of concentrate and forage. During the last 4 months, animals are on pasture. In order to simplify the calculation, it is assumed that during the 7 months, the diet is a mixed ration of concentrate and of a very digestible forage (value of buffer: 0.95 UEB per kg of dry matter of forage). As forage is very digestible, a substitution rate of -0.5 kg of forage per kilogram of concentrate must be taken into account. Under these assumptions, the 3.6 additional UFL can be provided by 1.5 kg dry matter of forage and 2.1 kg concentrate if their respective energy contents are 0.83 UFL and 1.12 UFL per kg. With a cost of forage equal to 0.2 FF per kg of dry matter and a cost of concentrate equal to 1.3 FF per kg, the marginal cost of 1 kg change in maternal effects on weaning weight is 3.0 FF.

Derivation of economic margins for suckler-fattening herds

Let y_1 be the average W210, y_2 be the average W500 and x be the daily postweaning gain, derived as $x = (y_2 - y_1)/290$. We denote by $W(t)$ the weight of the calf at a day t between 210 and 500 d. Assuming a linear growth during this period, $W(t) = y_1 + x(t - 210)$.

Production costs (c) of a calf sold at 500 d can be split in 2 parts: costs before weaning (c_1) and costs after weaning (c_2), such that $c = c_1 + c_2$. Costs before weaning are assumed to be the same as for suckler herds (see above). Costs after weaning are derived from

formulae established by INRA (1988) which calculate maintenance and growth costs at time t ($c_2(t)$) as a function of growth rate (x) and of metabolic weight ($W(t)^{0.75}$) of the animal:

$$c_2 = \sum_{t=210}^{500} c_2(t) \quad \text{with} \quad c_2(t) = p(a + bx^{1.4}) W(t)^{0.75} \quad \text{in FF/d}$$

where p is the price of 1 UFV (French energy units for growing cattle); a and b are coefficients calculated by INRA (1978) and depend on breed, sex and kind of production. For a young bull, a and b are respectively equal to 0.0502 and 0.0363; for a heifer, the corresponding values are 0.0472 and 0.0232.

Following the data collected by Aranyoss and Kontro (1991), we assume that both heifers and young bulls are fed a mixed ration containing 5.4 kg dry matter of maize silage (with 0.8 UFV/kg) and 2.1 kg concentrate (with 1.2 UFV/kg). The cost of 1 kg dry matter of maize silage is 0.67 FF and the cost of 1 kg concentrate is 1.11 FF. Finally, the price p of 1 UFV is 0.87 FF.

• The economic margin a_{f_2} for direct effects on final weight (A500) in a suckler-fattening herd is equal to 11.5 FF per kg.

The average price per kg of a calf sold at 500 d is 16.4 FF (table I). The marginal cost of one unit change in A500 is 6.1 FF for a male and 3.5 FF for a female. Thus, the average marginal cost is 4.9 FF. It is calculated from the following equations:

$$\frac{\partial c}{\partial g_2} = \frac{\partial c_2}{\partial x} \frac{\partial x}{\partial g_2} = \frac{1}{290} \frac{\partial c_2}{\partial x}$$

$$\frac{\partial c_2}{\partial x} = \frac{\partial \left(\sum_{t=210}^{500} p(a + bx^{1.4}) W(t)^{0.75} \right)}{\partial x} = p [0.75(a + bx^{1.4}) S_1 + 1.4bx^{1.4} S_2]$$

$$\text{with } S_1 = \sum_{j=0}^{290} j(y_1 + jx)^{-0.25} \quad \text{and} \quad S_2 = \sum_{j=0}^{290} (y_1 + jx)^{0.75}$$

• Let a_{d_2} and a_{m_2} be the economic weights for respectively direct and maternal effects on weaning weight in a suckler-fattening herd; $a_{d_2} = -4.8$ FF per kg and $a_{m_2} = -1.3$ FF per kg.

$$a_{d_2} = -\frac{\partial c}{\partial g_1} = -\left(6.5 + \frac{\partial c_2}{\partial g_1}\right) \quad \text{and} \quad a_{m_2} = -\frac{\partial c}{\partial g_1} = -\left(3.0 + \frac{\partial c_2}{\partial g_1}\right)$$

The marginal cost after weaning of one unit change in W210 (whatever the origin, either A210 or M210) is -2.5 FF for a male and -0.9 FF for a female. Thus, the average marginal cost is -1.7 FF. For a given weight at 500 d, a larger weaning weight leads to a smaller daily postweaning gain (x) and thus, to a smaller food requirement for postweaning growth.

APPENDIX III. Derivation of the sampling covariance matrix of REML estimators

Model and notations

$$\mathbf{y} = \begin{pmatrix} \mathbf{y}_{11} \\ \mathbf{y}_{12} \\ \mathbf{y}_{21} \\ \mathbf{y}_{22} \end{pmatrix} = \begin{bmatrix} \mathbf{1}_n & & & \\ & \mathbf{1}_n & & \\ & & \mathbf{1}_n & \\ & & & \mathbf{1}_n \end{bmatrix} \cdot \begin{pmatrix} \mu_{11} \\ \mu_{12} \\ \mu_{21} \\ \mu_{22} \end{pmatrix} + \begin{bmatrix} \mathbf{Z}_s & \mathbf{Z}_t & & & & & & & \\ & & \mathbf{Z}_s & \mathbf{Z}_t & & & & & \\ & & & & \mathbf{Z}_s & \mathbf{Z}_t & & & \\ & & & & & & \mathbf{Z}_s & \mathbf{Z}_t & \\ & & & & & & & & \mathbf{Z}_s & \mathbf{Z}_t \end{bmatrix} \cdot \begin{pmatrix} \mathbf{S}_{11} \\ \mathbf{t}_{11} \\ \mathbf{s}_{12} \\ \mathbf{t}_{12} \\ \mathbf{s}_{21} \\ \mathbf{t}_{21} \\ \mathbf{s}_{22} \\ \mathbf{t}_{22} \end{pmatrix} + \begin{pmatrix} \mathbf{e}_{11} \\ \mathbf{e}_{12} \\ \mathbf{e}_{21} \\ \mathbf{e}_{22} \end{pmatrix}$$

where, for trait i ($i = 1$ is W120; $i = 2$ is W210) and for the progeny j th generation: \mathbf{y}_{ij} , vector of records; μ_{ij} , mean of records taking into account the average genetic level of dams for each progeny generation; \mathbf{e}_{ij} , vector of residuals; \mathbf{s}_{ij} , vector of sire effects; \mathbf{t}_{ij} , vector of maternal grandsire (MGS) effects; \mathbf{Z}_s , incidence matrix for sire effects; \mathbf{Z}_t , incidence matrix for MGS effects.

Furthermore, we define c , the total number of traits; n , the number of records per trait and generation; N , the total number of records per trait ($N = 2n$); p , the number of bulls evaluated as sire and MGS; m , the number of records per bull ($n = pm$); d , the number of records per couple sire-MGS ($m = dp$); \mathbf{X} , the incidence matrix of fixed effects; \mathbf{Z} , the incidence matrix of genetic effects; \mathbf{R} , the residual variance-covariance matrix; \mathbf{G} , the genetic variance-covariance matrix; and \mathbf{V} , the phenotypic variance-covariance matrix.

The incidence matrices are $\mathbf{X} = \mathbf{I}_{2c} \otimes \mathbf{1}_n$, $\mathbf{Z} = \mathbf{I}_{2c} \otimes \mathbf{A}$ with $\mathbf{A} = (\mathbf{Z}_s \mathbf{Z}_t)$. The variance matrices are $\mathbf{R} = \mathbf{R}_0 \otimes \mathbf{I}_N$ where \mathbf{R}_0 is a $c \times c$ matrix, $\mathbf{G} = \mathbf{G}_0 \otimes \mathbf{I}_p$ where \mathbf{G}_0 is a $4c \times 4c$ matrix; $\mathbf{V} = \mathbf{Z}'\mathbf{G}\mathbf{Z} + \mathbf{R}$. \otimes stands for the direct product.

General results

The asymptotic sampling variance-covariance matrix $\text{Var}(\hat{\boldsymbol{\theta}})$ is given as the inverse of Fisher's information matrix $\mathbf{I}(\boldsymbol{\theta})$ (Searle *et al.*, 1992);

$$\text{Var}(\hat{\boldsymbol{\theta}}) = \mathbf{I}(\boldsymbol{\theta})^{-1} \quad \text{with} \quad \mathbf{I}(\boldsymbol{\theta}) = - \left\{ E \left(\frac{\partial^2 L}{\partial \theta_i \partial \theta_j} \right) \right\}_{i,j}$$

where L is the log likelihood of the multivariate normal density function,

$$\text{with} \quad E \left(\frac{\partial^2 L}{\partial \theta_i \partial \theta_j} \right) = -\frac{1}{2} \text{tr} \left[\mathbf{P} \frac{\partial \mathbf{V}}{\partial \theta_i} \mathbf{P} \frac{\partial \mathbf{V}}{\partial \theta_j} \right] \quad \text{and} \quad \mathbf{P} = \mathbf{V}^{-1} - \mathbf{V}^{-1} \mathbf{X} (\mathbf{X}' \mathbf{V}^{-1} \mathbf{X})^{-1} \mathbf{X}' \mathbf{V}^{-1}$$

Another form of the \mathbf{P} matrix has been derived by Harville (1977) and was used in our demonstration:

$$\mathbf{P} = \mathbf{S} - \mathbf{S} \mathbf{Z} \mathbf{W}^{-1} \mathbf{Z}' \mathbf{S} \quad \text{with} \quad \mathbf{W} = \mathbf{Z}' \mathbf{S} \mathbf{Z} + \mathbf{G}^{-1} \quad \text{and} \quad \mathbf{S} = \mathbf{R}^{-1} - \mathbf{R}^{-1} \mathbf{X} (\mathbf{X}' \mathbf{R}^{-1} \mathbf{X})^{-1} \mathbf{X}' \mathbf{R}^{-1}$$

Simplified form of S and W matrices due to our structure of data

Let us define $\mathbf{M}_n = \mathbf{I}_n - \frac{1}{n}\mathbf{J}_n$, an idempotent matrix. Then, $\mathbf{S} = \mathbf{R}_0^{-1} \otimes \mathbf{I}_c \otimes \mathbf{M}_n$

$$\mathbf{W} = \mathbf{Z}'\mathbf{S}\mathbf{Z} + \mathbf{G}^{-1} \quad \text{with} \quad \mathbf{Z}'\mathbf{S}\mathbf{Z} = (\mathbf{R}_0^{-1} \otimes \mathbf{I}_c) \otimes (\mathbf{A}'\mathbf{M}_n\mathbf{A})$$

then $\mathbf{W} = m\mathbf{R}_0^{-1} \otimes \mathbf{I}_c \otimes \mathbf{I}_2 \otimes \mathbf{M}_p + \mathbf{G}_0^{-1} \otimes \mathbf{I}_p$

thus $\mathbf{W}^{-1} = \mathbf{W}_1 \otimes \mathbf{I}_p + \mathbf{W}_2 \otimes \mathbf{J}_p$, where \mathbf{W}_1 and \mathbf{W}_2 can be easily calculated.

Results of the derivation of traces

Let $\mathbf{E}_0 = m\mathbf{R}_0^{-1} \otimes \mathbf{I}_{2c}$ and $\mathbf{W}_0 = \mathbf{E}_0 - \mathbf{E}_0\mathbf{W}_1\mathbf{E}_0$.

Between genetic components (t_1)

$$t_1 = (p-1) \cdot \text{tr} [\mathbf{W}_0\mathbf{D}_i\mathbf{W}_0\mathbf{D}_j]$$

because $\frac{\partial \mathbf{V}}{\partial \theta_i} = \mathbf{Z}' \frac{\partial \mathbf{G}}{\partial \theta_i} \mathbf{Z}$ and $\frac{\partial \mathbf{G}}{\partial \theta_i} = \mathbf{D}_i \otimes \mathbf{I}_p$ for any genetic variance components θ_i .

Between genetic component and residual component (t_2)

$\frac{\partial \mathbf{V}}{\partial \theta_i} = \frac{\partial \mathbf{R}}{\partial \theta_i} = \frac{\partial \mathbf{R}_0}{\partial \theta_i} \otimes \mathbf{I}_p$ for any residual variance component θ_i

$$t_2 = (p-1) \cdot \text{tr} \left[\mathbf{W}_0\mathbf{D}_j\mathbf{G}_0^{-1}\mathbf{W}_1 \left(\left(\mathbf{R}_0^{-1} \frac{\partial \mathbf{R}_0}{\partial \theta_i} \right) \otimes \mathbf{I}_{2c} \right) \right]$$

Between residual components (t_3)

The following matrices are partitioned in c^2 blocks:

$$\mathbf{R}^{-1} = \{\boldsymbol{\varepsilon}_{ij}\} \quad \mathbf{S} = \{\mathbf{S}_{ij}\} \quad \mathbf{S}\mathbf{Z} = \{\mathbf{B}_{ij}\} \quad \mathbf{W}^{-1} = \{\mathbf{W}_{ij}\}$$

$$\mathbf{P} = \{\mathbf{P}_{ij}\} \quad \mathbf{C} = \{\mathbf{C}_{ij}\} = \mathbf{S}\mathbf{Z}\mathbf{W}^{-1}\mathbf{Z}'\mathbf{S}$$

t_3 is a sum of traces of products $\mathbf{P}_{ij}\mathbf{P}_{kl}$ such that:

$$\text{tr} (\mathbf{P}_{ij}\mathbf{P}_{kl}) = \text{tr} (\mathbf{S}_{ij}\mathbf{S}_{kl}) - \text{tr} (\mathbf{S}_{ij}\mathbf{C}_{kl}) - \text{tr} (\mathbf{C}_{ij}\mathbf{S}_{kl}) + \text{tr} (\mathbf{C}_{ij}\mathbf{C}_{kl})$$

All these traces can be calculated as sums of traces of products of matrices of maximal size $2c \times 2c$.