

Multivariate restricted maximum likelihood estimation of genetic parameters for growth, carcass and meat quality traits in French Large White and French Landrace pigs

A Ducos¹, JP Bidanel¹, V Ducrocq¹,
D Boichard¹, E Groeneveld²

¹ INRA, Station de Génétique Quantitative et Appliquée,
Centre de Recherche de Jouy-en-Josas, 78352 Jouy-en-Josas Cedex, France;

² IAHHB, Federal Research Centre, 3057 Neustadt 1, Germany

(Received 22 February 1993; accepted 3 May 1993)

Summary – Genetic parameters of 7 traits measured in central test stations – average daily gain (ADG1), feed conversion ratio (FCR) and backfat thickness (ABT) measured on candidates for selection, and average daily gain (ADG2), dressing percentage (DP), estimated carcass lean content (ECLC) and meat quality index (MQI) measured in slaughtered relatives – were estimated for the Large White (LW) and French Landrace (LR) breeds using a derivative free restricted maximum likelihood (DF-REML) procedure applied to a multiple trait individual animal model. The data consisted of 2 sets of records (3 671 and 3 630 candidates, 3 039 and 2 695 slaughtered animals in, respectively, LW and LR breeds) collected at 3 different stations from 1985–1990 (LW) or 1980–1990 (LR). The models included additive genetic value, common environment of birth litter and residual random effects, a fixed year × station × batch or year × station × slaughter date effect and, for traits measured in slaughtered animals, a fixed sex effect and a covariable (weight at the beginning or at the end of the test period). Heritabilities of ADG1, ABT, FCR, ADG2, DP, ECLC and MQI were respectively 0.30, 0.64, 0.22, 0.52, 0.39, 0.60, 0.33 in the LW and 0.34, 0.56, 0.25, 0.46, 0.31, 0.68, 0.23 in the LR breed. Common litter effects ranged from 5% (ABT in LW breed) to 16% (ADG2 in LR breed) of phenotypic variance. Growth traits and FCR exhibited favourable genetic correlations, but were unfavourably correlated to DP and carcass lean content. MQI also showed unfavourable though generally low genetic correlations with all the other traits. These antagonisms were apparent in both breeds, but tended to be larger in the LW than in the LR breed.

pig / genetic parameter / restricted maximum likelihood / growth / carcass / meat quality

Résumé – Estimation des paramètres génétiques des caractères de croissance, de carcasse et de qualité de la viande dans les races Large White et Landrace français par la méthode du maximum de vraisemblance restreinte appliquée à un modèle animal multicaractère. Les paramètres génétiques de sept caractères mesurés dans les stations publiques de contrôle de performance – le gain moyen quotidien (GMQ1), l'indice de consommation (IC) et l'épaisseur de lard (ELD) mesurés sur les candidats à la sélection ainsi que le gain moyen quotidien (GMQ2), le rendement de carcasse (RDT), le pourcentage de muscle (PM) et l'indice de qualité de la viande (IQV) mesurés sur des apparentés abattus – ont été estimés pour les races Large White (LW) et Landrace français (LR) à l'aide du maximum de vraisemblance restreinte appliqué à un modèle animal multicaractères. Deux fichiers de tailles comparables (3 671 et 3 630 candidats, 3 039 et 2 695 animaux abattus, respectivement, pour les races LW et LR) ont été constitués à partir des données collectées dans trois stations au cours des périodes 1985-90 (LW) et 1980-90 (LR). Les modèles d'analyse incluaient les effets aléatoires de la valeur génétique additive de l'animal, du milieu commun de la portée de naissance, l'effet fixé de l'année \times station \times bande ou de l'année \times station \times date d'abattage et, pour les caractères mesurés chez les animaux abattus, l'effet fixé du sexe et une covariable (poids au début ou à la fin du contrôle). Les valeurs d'héritabilité de GMQ1, ELD, IC, GMQ2, RDT, PM et IQV s'élèvent respectivement à 0,30; 0,64; 0,22; 0,52; 0,39; 0,60; 0,33 en race LW et 0,34; 0,56; 0,25; 0,46; 0,31; 0,68; 0,23 en race LR. Les effets de milieu commun de la portée de naissance représentent de 5% (ELD en race LW) à 16% (GMQ2 en race LR) de la variance phénotypique. La croissance et l'indice de consommation présentent entre eux des corrélations génétiques favorables, mais sont corrélés de façon défavorable au rendement et au taux de muscle de la carcasse. L'IQV présente également des corrélations génétiques défavorables, bien qu'en général faibles, avec l'ensemble des autres caractères. Ces antagonismes existent dans les deux races, mais tendent à être plus marqués en race LW que LR.

porcin / paramètre génétique / maximum de vraisemblance restreinte / croissance / carcasse / qualité de la viande

INTRODUCTION

Best linear unbiased prediction (BLUP) applied to an individual animal model (IAM; Henderson, 1988) is becoming increasingly used to predict breeding values in most species of farm animals (Carabano and Alenda, 1990). In pigs, numerous studies have been conducted to evaluate the advantage of using BLUP instead of standard selection indexes in a variety of situations (Belonsky and Kennedy, 1988; Keele *et al*, 1988; Sorensen, 1988; Wray, 1989; Long *et al*, 1990; De Vries *et al*, 1990; Roehe *et al*, 1990). National genetic evaluation programmes based on the BLUP-IAM technique have been implemented in several countries since 1985 (Hudson and Kennedy, 1985; Van Hofstraeten and Vandepitte, 1988; Harris *et al*, 1989; Sorensen and Vernessen, 1991). In France, a national genetic evaluation programme based on BLUP-IAM methodology is being implemented for both production and reproduction traits. The first step of this project concerns the genetic evaluation of station tested animals, *ie* \approx 6 000 animals/yr.

The use of BLUP procedures requires knowledge of variance components in the unselected base population. In practice, these components have to be estimated

from available data. The method of restricted maximum likelihood (REML; Patterson and Thompson, 1971) has been shown to be the method of choice for estimating variance components in selected populations, mainly because of its ability to account for selection bias (Gianola *et al.*, 1986). The aim of this study is to estimate genetic parameters of French Large White and Landrace breeds for traits measured in central test stations using a multiple trait IAM-REML.

MATERIAL

Animals and data recording

Genetic evaluation of centrally tested pigs in France is currently based on a combined selection index involving performance of the candidate for selection and of 1 full-sib. Full-sibs are females or barrows castrated before entering the station, *ie* shortly after weaning. Breeders are asked to choose centrally tested animals at random in litters of at least 8 piglets. The data analysed in the present study concerned both candidates for selection and relatives slaughtered at the end of test. In order to keep computing costs reasonable, 2 computationally manageable sets of data (*ie* 3 671 and 3 630 candidates, 3 039 and 2 695 relatives in, respectively, LW and LR breeds) were created by considering all the data collected in the 3 stations in which both candidates for selection and relatives were tested. The period of time considered was 1985–1990 for the LW and 1980–1990 for the LR. For computational reasons, only 2 generations of ancestors, *ie* the parents and grand-parents of tested animals, were considered. The structure of the 2 data sets is shown in table I.

Table I. Structure of the 2 data sets analysed.

<i>Pigs tested</i>	<i>Large White</i>		<i>French Landrace</i>	
	<i>Candidates</i> 3 671	<i>Relatives</i> 3 039	<i>Candidates</i> 3 630	<i>Relatives</i> 2 695
Ancestors (parents + grand-parents)	4 628 ^a	4 281 ^a	4 586 ^b	4 030 ^b
No of year × station × batch (YSB)	94	81	130	122
Tested pigs/YSB	39.05	37.52	27.92	22.09
No of year × station × slaughter date (YSS)	–	221	–	251
Tested pigs/YSS	–	13.75	–	10.74
No of litters	2 404 ^c	2 136 ^c	2 509 ^d	1 770 ^d
Tested pigs/litter	1 = 53% 2 = 43% > 2 = 4%	1 = 59% 2 = 41% > 2 = 0.5%	1 = 60% 2 = 35% > 2 = 5%	1 = 48% 2 = 52% > 2 = 0%

^a 1 562 common ancestors; ^b 1 965 common ancestors; ^c 909 common litters; ^d 545 common litters.

Testing of both candidates for selection and their relatives was performed in discontinuous batches. A batch was defined by the year of test, the testing station and the 2-wk period of entering station (≈ 4 levels for each year \times station combination) and will consequently be referred to as the year \times station \times batch ($Y \times S \times B$) effect hereafter.

Young boars were tested between 35 and 90 kg live weight. Until 1988, they were penned in groups of 4, but individually fed on a liberal feeding diet based on the voluntary feed intake of the animal during 2 daily meals of 20 min each. From 1988 they were allotted to pens of 10–12 animals, with *ad libitum* feeding. Animals were weighed twice at the beginning and at the end of the test. Dates of measurement were chosen so that the 2 initial and the 2 final weights flanked 35 and 90 kg, respectively. This allowed us to adjust the different traits to a constant initial and/or final weight. Feed intake was recorded individually during the whole test until 1988. Backfat thickness was measured twice at the same time as final weights. The ultrasonic measurements were taken on each side of the spine, 4 cm from the mid-dorsal line at the levels of the shoulder, the last rib and the hip joint, respectively.

Animals from the second group were tested between 35 and 100 kg live weight. They were allotted to pens of 2 animals until 1988, and to pens of 10–12 animals thereafter. Pigs were fed *ad libitum*, but feed intake was not individually recorded. Animals were weighed once ≈ 35 kg and twice ≈ 100 kg. They were slaughtered during the week following the last weight measurement. Standardized cutting of one half-carcass was performed as described by Ollivier (1970) until 1988, and since 1989 as described in Anonymous (1990).

Three measurements of meat quality were taken on the ham on the day after slaughter, *ie*: 1) ultimate pH (pHu) of Adductor femoris muscle; 2) water-holding capacity (WHC) as assessed by the time (in tens of s) for a piece of pH paper to become wet when put on the freshly cut surface of Biceps femoris (until 1988) or Gluteus superficialis (since 1989) muscle; 3) reflectance (REF) of Gluteus superficialis muscle at 630 nm, using a Manuflex reflectometer (scale 0 to 1 000).

Traits analyzed

Seven different traits were defined from the above-mentioned measurements:

– average daily gain (ADG1) and feed conversion ratio (FCR) from 35 to 90 kg and backfat thickness at 90 kg (ABT) of young boars candidates for selection. Adjustments to a constant initial and/or final weight were made by interpolation between the 2 weights flanking 35 and/or 90 kg, respectively;

– average daily gain from 35 to 100 kg (ADG2), dressing percentage (DP), estimated carcass lean content (ECLC) of the carcass with head (EC reference) and meat quality index (MQI) of candidates' relatives. DP was computed as the ratio of carcass weight with head and feet to live weight. ECLC was estimated from the relative weight of 6 joints expressed as percentage of half-carcass weight, according to the following prediction equations: [1] $ECLC1 = -3.539 + 0.751$ (percentage of ham) + 1.216 (percentage of loin) – 0.610 (percentage of backfat) – 0.453 (percentage of leaf fat) + 0.328 (percentage of belly); [2] $ECLC2 = -42.035 + 1.282$ (percentage of ham) + 1.818 (percentage of loin) – 0.678 (percentage of

backfat) + 0.040 (percentage of leaf fat) + 0.701 (percentage of belly) + 0.616 (percentage of shoulder). Equation [1] was used until 1988 and was replaced by equation [2] simultaneously with the change in cutting procedure. Both equations have been shown to be highly correlated with the true carcass lean content ($R^2 = 0.911$ for the first equation and 0.930 for the second) so that ECLC1 and ECLC2 were considered as the same trait. The meat quality index (MQI), established as a predictor of the technological yield of Parisian ham processing, was computed as a linear function of the 3 meat quality measurements defined above (Guéblez *et al.*, 1990): $MQI = -35 + 8.329 \text{ pHu} + 0.127 \text{ WHC} - 0.00744 \text{ REF}$. Elementary statistics for the 7 traits studied are shown in table II.

METHODS

Model

The model varied according to the trait, but had the following basic structure (in matrix notation):

$$y = Xb + Wp + Za + e \quad [1]$$

where y is the vector of observations for the 7 traits, b is the vector of fixed effects, p is the vector of litter effects, a is the vector of additive genetic values of animals, e is the vector of residuals and X , W , Z are incidence matrices relating observations to the effects in the model. Location and dispersion parameters for the random effects were as follows:

$$E \begin{bmatrix} y \\ e \\ p \\ a \end{bmatrix} = \begin{bmatrix} Xb \\ 0 \\ 0 \\ 0 \end{bmatrix} \quad \text{Var} \begin{bmatrix} y \\ e \\ p \\ a \end{bmatrix} = \begin{bmatrix} V & R & WG_p & ZG_a \\ R & R & 0 & 0 \\ G_p W' & 0 & G_p & 0 \\ G_a Z' & 0 & 0 & G_a \end{bmatrix} \quad [2]$$

where:

$$V = R + ZG_a Z' + WG_p W'$$

$$R = \bigoplus_{j=1}^m R_{o_{ij}}, \text{ with } m = \text{number of records and } i = \text{pattern of missing values,}$$

$$G_p = I_p \otimes G_{op}$$

$$G_a = A \otimes G_{oa}$$

A = numerator relationship matrix,

G_{oa} = variance-covariance matrix for the additive genetic effect,

G_{op} = variance-covariance matrix for the effect,

$R_{o_{ij}}$ = residual covariance matrix for animal j with a pattern i of missing values,

\otimes = Kronecker product,

\oplus = direct sum.

The exact model used for each of the 7 traits is shown in table III. ADG2 was not pre-adjusted for initial weight, which was consequently included as a covariable

Table II. Number of pigs (*N*), means and phenotypic standard deviations (σ_P) for the 7 traits studied.

<i>Type of animal</i>	<i>Trait</i>	<i>Large White</i>			<i>French Landrace</i>		
		<i>N</i>	<i>Mean</i>	σ_P	<i>N</i>	<i>Mean</i>	σ_P
Candidates for selection	Average daily gain (g/d)	3 671	972	83	3 630	869	73
	Average backfat thickness (mm)	3 671	12.0	1.6	3 630	13.4	1.6
	Feed conversion ratio (kg/kg)	2 374	2.49	0.17	2 974	2.70	0.21
Slaughtered relatives	Average daily gain (g/d)	3 039	898	96	2 695	845	84
	Dressing percentage (%)	3 039	79.0	1.5	1 338	78.0	1.6
	Estimated carcass lean content (%)	3 039	51.0	3.6	2 695	49.8	3.2
	Meat quality index (point)	2 907	11.7	2.5	2 205	11.7	2.6

in the model for that trait. Year \times station \times slaughter date has been shown to be the most important environmental factor affecting meat quality traits (Monin, 1983) and was therefore included as a fixed effect in the model for MQI instead of $Y \times S \times B$.

Computing strategies

The (co)variance components were estimated using the derivative free multiple trait restricted maximum likelihood procedure described by Groeneveld (1991).

It was not possible computationally to analyse all traits simultaneously and only 2-trait analyses reached convergence at a reasonable computing cost. Hence, 21 2-trait analyses were performed for each breed. A derivative-free Quasi-Newton (DF-QN) algorithm was used to maximise the likelihood when possible because of its good convergence rate. The subroutine E04JAF from the NAG library (Numerical Algorithms Group, 1990) was used for this purpose. The convergence criterion was defined as the standardized norm of the changes in variance components between 2 consecutive iterations. The stopping criterion was set at 10^{-7} . However, convergence could not be reached in all cases. The DF-QN procedure approximates the matrix of the second derivatives (Hessian matrix) by finite difference and works relatively well for smooth portions of the likelihood function with continuous derivatives. But when one of the parameters is located at the border of the parameter space, adding a finite difference may generate numerical values outside the parameter space, in which case DF-QN does not work. When this situation occurred, the DF-QN algorithm was replaced by a Downhill Simplex based algorithm (Press and Flannery, 1986). Being a sampling procedure, Downhill Simplex can handle values outside the parameter space much better, thus finding the optimum where gradient based optimisers fail (Kovac, 1992). The convergence criterion was determined as the fractional range from the highest to the lowest likelihood value of the vertex (Groeneveld, 1991). The stopping criterion was set at 10^{-4} .

Approximate asymptotic standard errors of variance components and genetic parameters were obtained from the approximate Hessian matrix computed by the Quasi-Newton E04JBF subroutine from the NAG library (Numerical Algorithms Group, 1990). These approximate standard errors are lower bounds of the standard errors for the parameter estimates (Gianola, 1989).

RESULTS

The Quasi-Newton algorithm was used for all pairs of traits except the (ADG1-ADG2) pair, which had convergence problems. Computing time on an IBM 3090-17T varied from 31 to 165 min of CPU time in the LW breed and from 32 to 172 min of CPU time in the LR breed. The Downhill Simplex algorithm was used for the (ADG1-ADG2) pair of traits. Computing times were 366 and 591 min of CPU time for LW and LR breeds, respectively.

Six estimates of variance components were available for each trait. Variation among estimates was small (variation coefficient of heritabilities was lower than 5%, in both breeds), so that only average values are presented (table IV). ABT and ECLC had the largest heritabilities (h^2) in both breeds. The LW had a higher

h^2 for ABT (0.64 *vs* 0.56), but a lower one for ECLC (0.60 *vs* 0.68) than the LR. ADG2 was much more heritable in both breeds than ADG1 (0.52 and 0.46 *vs* 0.30 and 0.34 in LW and LR, respectively). Heritability values were very similar in the 2 breeds for FCR, but larger in the LW breed for DP and MQI (0.39 *vs* 0.31 and 0.33 *vs* 0.23). Common environmental effects were not negligible for all the traits, with estimates ranging from 5 to 16% of the phenotypic variance. The largest values were obtained for growth rate and, in the LR breed, for MQI. Differences between breeds were small, except for ABT (0.05 *vs* 0.12) and MQI (0.06 *vs* 0.15).

Table IV. Estimates of heritability and common environmental effects in Large White and French Landrace breeds.

Trait	Breed			
	Large White		French Landrace	
	$h^2 \pm SE^a$	$c^2 \pm SE^a$	$h^2 \pm SE^a$	$c^2 \pm SE^a$
Candidates for selection				
Average daily gain (g/d)	0.30 \pm 0.02	0.14 \pm 0.02	0.34 \pm 0.02	0.14 \pm 0.02
Average backfat thickness (mm)	0.64 \pm 0.01	0.05 \pm 0.01	0.56 \pm 0.01	0.12 \pm 0.01
Feed conversion ratio (kg/kg)	0.22 \pm 0.02	0.09 \pm 0.02	0.25 \pm 0.02	0.12 \pm 0.02
Slaughtered relatives				
Average daily gain (g/d)	0.52 \pm 0.02	0.14 \pm 0.02	0.46 \pm 0.02	0.16 \pm 0.02
Dressing percentage (%)	0.39 \pm 0.02	0.06 \pm 0.02	0.31 \pm 0.02	0.06 \pm 0.02
Estimated carcass lean content (%)	0.60 \pm 0.02	0.13 \pm 0.02	0.68 \pm 0.02	0.09 \pm 0.02
Meat quality index (point)	0.33 \pm 0.02	0.06 \pm 0.02	0.23 \pm 0.02	0.15 \pm 0.02

^a Heritability (h^2) and common environmental effect (c^2) \pm standard error.

Estimates of genetic and phenotypic correlations for the LW and LR breeds are shown in tables V and VI, respectively. Genetic correlations were well estimated for traits measured on the same animals but had larger standard errors for traits measured on different animals. Genetic correlations between ADG1 and ADG2 were close to unity in both breeds (0.97 and 0.99 in LW and LR breeds, respectively). Similarly, traits predicting carcass lean content, *ie* ABT in candidates and ECLC in relatives were highly correlated (-0.86 and -0.90 in LW and LR breeds, respectively). Growth traits and FCR were negatively, *ie* favourably, correlated (-0.61 and -0.63 on average for ADG1 and ADG2, respectively) but showed unfavourable genetic correlations with carcass traits. Genetic correlations between MQI and growth or carcass traits were generally low, but were unfavourable in both breeds. Some correlations differed between breeds. This was particularly the case for the correlations between MQI and ECLC (-0.44 in LW *vs* -0.02 in LR), ADG2 and DP (0.08 in LW *vs* -0.53 in LR) or ADG1 and ABT (0.48 in LW *vs* 0.25 in LR). In general, the antagonisms between carcass lean content on one hand, growth rate and meat quality on the other hand, tended to be larger in the LW breed than in the LR breed.

Table V. Estimates of genetic (above diagonal) and phenotypic (below diagonal) correlations in the Large White breed.

<i>Traits</i>	<i>Average daily gain</i>	<i>Backfat thickness</i>	<i>Feed conversion ratio</i>	<i>Average daily gain</i>	<i>Dressing percentage</i>	<i>Estimated carcass lean content</i>	<i>Meat quality index</i>
Candidates for selection							
Average daily gain	-	0.48 ± 0.04	-0.49 ± 0.02	0.97 ± 0.07	-0.19 ± 0.09	-0.25 ± 0.08	-0.04 ± 0.10
Average backfat thickness	0.24 ± 0.02	-	0.27 ± 0.04	0.21 ± 0.07	0.08 ± 0.07	-0.86 ± 0.05	0.06 ± 0.08
Feed conversion ratio	-0.76 ± 0.01	0.07 ± 0.02	-	-0.69 ± 0.07	0.01 ± 0.11	-0.41 ± 0.10	0.25 ± 0.12
Relatives of candidates							
Average daily gain	-	-	-	-	0.08 ± 0.03	-0.09 ± 0.03	0.00 ± 0.05
Dressing percentage	-	-	-	-0.20 ± 0.02	-	0.05 ± 0.03	-0.17 ± 0.04
Estimated carcass lean content	-	-	-	-0.19 ± 0.02	-0.01 ± 0.02	-	-0.44 ± 0.04
Meat quality index	-	-	-	-0.03 ± 0.03	0.00 ± 0.02	-0.08 ± 0.02	-

Table VI. Estimates of genetic (above diagonal) and phenotypic (below diagonal) correlations in the French Landrace breed.

<i>Traits</i>	<i>Average daily gain</i>	<i>Backfat thickness</i>	<i>Feed conversion ratio</i>	<i>Average daily gain</i>	<i>Dressing percentage</i>	<i>Estimated carcass lean content</i>	<i>Meat quality index</i>
Candidates for selection	-	0.25 ± 0.03	-0.76 ± 0.02	0.99 ± 0.08	-0.03 ± 0.12	-0.10 ± 0.07	-0.05 ± 0.13
Average daily gain	0.11 ± 0.02	-	0.27 ± 0.04	-0.01 ± 0.07	0.13 ± 0.11	-0.90 ± 0.03	0.17 ± 0.11
Average backfat thickness	-0.76 ± 0.01	0.16 ± 0.02	-	-0.54 ± 0.12	-0.12 ± 0.20	-0.22 ± 0.10	0.34 ± 0.18
Feed conversion ratio	-	-	-	-	-0.53 ± 0.06	-0.06 ± 0.03	-0.19 ± 0.07
Relatives of candidates	-	-	-	-0.13 ± 0.02	-	-0.07 ± 0.04	-0.01 ± 0.09
Average daily gain	-	-	-	-	-0.08 ± 0.03	-	-0.02 ± 0.04
Dressing percentage	-	-	-	0.06 ± 0.03	0.04 ± 0.04	-0.07 ± 0.03	-
Estimated carcass lean content	-	-	-	-	-	-	-
Meat quality index	-	-	-	-	-	-	-

DISCUSSION

Methodology

There is general agreement that BLUP and REML methodologies using an animal model are the methods of choice for estimating location and dispersion parameters for traits that can be described by linear models, because of their desirable statistical and genetic properties (Harville, 1977; Kennedy *et al*, 1988; Robinson, 1991). In particular, this method accounts for the effects of selection if all the information related to selection is included in the analysis.

Practical applications of BLUP-IAM in pig breeding are steadily increasing. Its use has been greatly facilitated over the last few years by the increasing power of computers and the appearance of general purpose software such as "PEST" (Groeneveld *et al*, 1990), or "PIGBLUP" (Brandt, 1990). On the other hand, the use of multivariate REML-IAM is still infrequent, mainly because of its huge computational requirements. Limited applications are possible but, in most cases, at the expense of some departures from the ideal situation. In the present case, a total of 72 (co)variances had to be estimated. A problem of comparable size (*ie* 60 covariance components) was treated by Groeneveld (1991), but with larger computing facilities and a more favourable data structure. The present data set had several drawbacks, such as different traits measured on different individuals, a low number of animals per parent and per litter, and a low number of performance-tested parents. Each of them resulted in convergence problems, which were solved by: 1) limiting the number of generations of ancestors; 2) putting the litter covariance component to zero; 3) running 2-trait analyses. Limiting the number of ancestors and decreasing the number of (co)variance components resulted in a reduction of the number of likelihood functions to be computed and of the CPU time per likelihood. The impact of 1) was investigated with univariate models. Adding a third generation of ancestors considerably increased computing time, but did not change variance components at all. The effect of 2) was investigated for the (ADG1, ABT) and (ECLC, ABT) pairs of traits. Non-negligible correlation for the litter effect was obtained in both cases (0.21 and 0.75, respectively). However, this was mainly due to the low magnitude of litter variances, litter covariance being much smaller ($< 1/10$) than genetic or residual covariances. As a consequence, the impact on the other covariance components and on predicted breeding values was very limited.

The impact of 3) was theoretically more critical. First, all traits selected upon should be included in the analysis to take into account properly the effects of selection. The effect of this simplification could not be tested, but the stability of estimates of variance components obtained from different 2-trait analyses tends to indicate that it should be rather limited, at least for variances. Then, the positive definiteness of the variance-covariance matrices is no longer guaranteed. Indeed, inconsistencies were obtained in both breeds. Yet they were mainly due to the (ADG1, ADG2) pair of traits, and positive definiteness was obtained when 1 of the 2 traits was removed from the matrix.

Another underlying assumption of the present REML analysis was the homogeneity of within-station variances. In fact, as first mentioned by Ollivier *et al*

(1981), noticeable differences in variability may exist between stations. Methods have recently been developed to estimate variance components in situations of heteroskedasticity (Foulley *et al*, 1990, 1992; San Cristobal, 1992). These methods are computationally much more demanding than standard REML and are currently intractable in applications such as the present one.

Genetic parameters

Genetic parameters in French LW and LR breeds using data from testing stations had previously been estimated by Ollivier (1970), Ollivier *et al* (1980, 1981), Tibau i Font and Ollivier (1984), Sellier *et al* (1985) and Cole *et al* (1988). All these studies used classical estimation methods such as parent-offspring regression or Henderson's methods (Henderson, 1953).

Heritability estimates are generally comparable to previous French studies and literature means (table VII). The only noticeable exceptions are the relatively low values obtained for FCR and the unusually large values obtained for ADG2 and ABT. Higher h^2 values for ADG2 as compared to ADG1 were not previously obtained by Ollivier *et al* (1980, 1981) and Tibau i Font and Ollivier (1984). This result suggests that growth rate is genetically more variable and more heritable under an *ad libitum* than under a restricted feeding diet. Variation in genetic parameter estimates due to feeding regime is well established in pigs (Wyllie *et al*, 1979; Cameron *et al*, 1988). As suggested by Cameron (1990), heritability estimates of ADG and ABT might be lower under a restricted feeding diet because competition effects would increase non-additive variance components. In spite of these heritabilities, feeding regime, sex and period of test differences, the 2 traits appeared as genetically very similar, the genetic correlation being very close to unity in both breeds. This result somewhat disagrees with the value of 0.55 reported by Tibau i Font and Ollivier (1984).

The signs of the genetic correlations are generally in good agreement with literature means (table VII). In general, the magnitude of these correlations is closer to previous French results and literature means in the LR than in the LW breed. Yet, several exceptions have to be mentioned. FCR and ECLC are less correlated than usually reported in the literature (-0.22 vs values ranging from -0.30 to -0.57 : Lundeheim *et al*, 1980; Ollivier *et al*, 1981; Tibau i Font and Ollivier, 1984; Costa *et al*, 1986; Johansson *et al*, 1987; Van Hofstraeten and Vandepitte, 1988). The lack of antagonism between ECLC and MQI disagrees with most literature results in the LR breed (Malmfors and Nilsson, 1979; Lundeheim *et al*, 1980; Ollivier, 1983; Andersen and Vestergaard, 1984; Busse and Groeneveld, 1986; Merks, 1987; Schwörer *et al*, 1987; Cole *et al*, 1988). Differences between estimates may be related to variations in the frequency of the halothane gene in the populations studied (Sellier, 1988). ABT and ECLC are more closely correlated in both breeds than in previous French studies (-0.38 ; Tibau i Font and Ollivier, 1984) or than the literature average (-0.65). The large negative correlation between ADG2 and DP is also in disagreement with the only available literature estimates (0.93 ± 0.05 ; Cameron, 1990; 0.36 ; Johansson *et al* 1987). There is no clear explanation for these large differences.

Discrepancies with literature means and previous French results are greater in the LW breed. The antagonism between growth rate and carcass composition,

Table VII. Average literature values^a (\pm SD) of genetic parameters for growth, carcass and meat quality traits (Ducos, submitted for publication).

	<i>Average daily gain on test</i>	<i>Backfat thickness</i>	<i>Feed conversion ratio</i>	<i>Carcass lean content^b</i>	<i>Meat quality^c</i>
Average daily gain on test	0.32 \pm 0.16 (132) ^d	0.17 \pm 0.28 (74)	-0.63 \pm 0.35 (46)	-0.05 \pm 0.29 (53)	-0.06 \pm 0.25 (65)
Backfat thickness		0.45 \pm 0.18 (143)	0.20 \pm 0.23 (34)	-0.65 \pm 0.24 (39)	0.16 \pm 0.24 (56)
Feed conversion ratio			0.33 \pm 0.13 (58)	-0.32 \pm 0.32 (30)	0.10 \pm 0.16 (25)
Carcass lean content				0.54 \pm 0.19 (77)	-0.21 \pm 0.21 (70)
Meat quality					0.24 \pm 0.15 (115)

^a Heritabilities on the diagonal, genetic correlations above the diagonal; ^b estimated carcass lean (fat) content, lean/fat ratio, premium cut percentage, loin or ham weight; ^c pH, reflectance, water-holding capacity or meat quality index; ^d number of estimations in brackets.

particularly between ADG1 and ABT, appears to be stronger than previously reported by Tibau i Font and Ollivier (1984), Kwon *et al* (1986), Van Steenberg *et al* (1989), and Kaplon *et al* (1991). However, literature estimates are quite variable and large unfavourable correlations were also reported in LW or Yorkshire by Merks (1987), Savoie and Minvielle (1988), and Johansson *et al* (1987). The correlations between growth rate and FCR also differ from usual patterns; the relationship between ADG and FCR is generally closer under a restricted feeding diet than with an *ad libitum* diet (Ollivier *et al*, 1980; Tibau i Font and Ollivier, 1984; Cameron *et al*, 1988). The lack of antagonism between growth rate and meat quality is in disagreement with most studies in the LW breed (Ollivier, 1983; Johansson *et al*, 1987; Cole *et al*, 1988). In contrast, the unfavourable correlation between MQI and ECLC is larger than those reported by Lundeheim *et al* (1980), Johansson *et al* (1987), or Cole *et al* (1988).

CONCLUSION

Accurate estimates of genetic parameters are essential to evaluate and compare alternative breeding plans as well as to predict breeding values. The genetic parameters estimated in the present study are likely to be more adequate than previous estimates, because multivariate REML-IAM procedures allow the fit of more realistic models, which are similar to those used for the genetic evaluation and give parameters which tend to be less biased by selection. However, multivariate REML-IAM procedures are computationally very demanding, so that only rather small data sets and only few traits (two in the present case) can be treated simultaneously. As a consequence, selection is probably not fully taken into account and variance-covariance matrices are less likely to be positive-definite. Better optimization algorithms, more powerful computers and better data structures will all be necessary to be able to run full multiple trait REML-IAM.

ACKNOWLEDGMENTS

We are indebted to the staff of central testing stations for collecting the data throughout the study period.

REFERENCES

- Andersen S, Vestergaard T (1984) Estimation of genetic and phenotypic parameters for selection index evaluation in the Danish pig breeding programme. *Acta Agric Scand* 343, 231-243
- Anonymous (1990) Résultats du 16^e test de contrôle des produits terminaux des schémas de sélection et de croisement. *Techni-Porc* 13(5), 44-45
- Anonymous (1992) Résultats du 17^e test de contrôle des produits terminaux des schémas de sélection et de croisement. *Techni-Porc* 15(2), 19-33
- Belonsky GM, Kennedy BW (1988) Selection on individual phenotype and best linear unbiased prediction of breeding values in a close swine herd. *J Anim Sci* 66, 1124-1131

- Brandt H (1990) Selection criteria using an animal model in pig breeding. *In: Commission on Animal Genetics: 41th Annu Meet Eur Assoc Anim Prod.* Toulouse, France, September 1990
- Busse W, Groeneveld E (1986) Estimation of population traits in German Landrace pigs on the basis of data from the Mariensee herdbook information system. *Züchtungskunde* 58, 175-183
- Cameron ND (1990) Genetic and phenotypic parameters for carcass traits, meat and eating quality traits in pigs. *Livest Prod Sci* 26, 119-135
- Cameron ND, Curran MK, Thompson R (1988) Estimation of sire with feeding regime interaction in pigs. *Livest Prod Sci* 26, 119-135
- Carabano MJ, Alenda R (1990) Serving several species with animal models. *In: 4th World Congr Genetics Appl Livestock Prod.* Edinburgh, UK, 23-27 July 1990, vol XVI, 395-399
- Cole G, Le Henaff G, Sellier P (1988) Paramètres génétiques de quelques caractères de qualité de la viande dans les races porcines Large White, Landrace Français et Landrace Belge. *In: 20^e Journées Rech Porcine en France.* Paris, 2-4 February 1988, Institut Technique du Porc, Paris, 249-254
- Costa CN, Saralegui WH, Favero JA, Leitao GR (1986) Genetic parameters and selection indices for pigs. *Rev Soc Bras Zootech* 15, 124-131
- De Vries AG, Van der Steen HAM, de Roo G (1990) Effects of family size in selection and testing in a closed line of pigs. *Livest Prod Sci* 24, 46-63
- Foulley JL, Gianola D, San Cristobal M, Im S (1990) A method for assessing extent and sources of heterogeneity of residual variances in mixed linear models. *J Dairy Sci* 73, 1612-1624
- Foulley JL, San Cristobal M, Gianola D, Im S (1992) Marginal likelihood and Bayesian approaches to the analysis of heterogeneous residual variances in mixed linear gaussian models. *Compt Stat Data Anal* 13, 291-305
- Gianola D, Foulley JL, Fernando RL (1986) Prediction of breeding values when variances are not known. *Genet Sel Evol* 18, 475-484
- Gianola D (1989) *Application of Bayesian methods in Animal Breeding. Course Notes.* INRA, Jouy-en-Josas, France
- Groeneveld E (1991) Simultaneous REML estimation of 60 covariance components in an animal model with missing values using the Downhill Simplex algorithm. *In: Commission on Animal Genetics: 42th Annu Meet Eur Assoc Anim Prod.* Berlin, Germany, September 1991
- Groeneveld E, Kovac M, Wang T (1990) PEST, a general purpose BLUP package for multivariate prediction and estimation. *In: 4th World Congr Genet Appl Livestock Prod.* Edinburgh, UK, 23-27 July 1990, vol XIII, 488-491
- Guéblez R, Le Maître C, Jacquet B, Zert P (1990) Nouvelles équations de prédiction du rendement technologique de la fabrication du jambon de Paris. *In: 22^e Journées Rech Porcine en France.* Paris, 30 January-1 February 1990, Institut Technique du Porc, Paris, 89-96
- Harris DL, Lofgren DL, Stewart TS, Schinckel AP (1989) Adapting Best Linear Unbiased Prediction (BLUP) for timely genetic evaluation. I. Progeny traits in a single contemporary group for each sex. *J Anim Sci* 67, 3209-3222
- Harville DA (1977) Maximum likelihood approaches to variance component estimation and to related problems. *J Am Stat Assoc* 72, 320-338

- Henderson CR (1953) Estimation of variance and covariance components. *Biometrics* 9, 226-252
- Henderson CR (1988) Theoretical basis and computational methods for a number of different animal models. *J Dairy Sci* 71 (suppl 2), 1-16
- Hudson GFS, Kennedy BW (1985) Genetic evaluation of swine for growth rate and backfat thickness. *J Anim Sci* 61, 83-91
- Johansson K, Andersson K, Lundeheim N (1987) Evaluation of station testing of pigs. 1. Genetic parameters for feed measurements and selection effects on voluntary feed intake. *Acta Agric Scand* 37, 93-107
- Kaplon MJ, Rothschild MF, Berger PJ, Healey M (1990) Population parameter estimates for performance and reproductive traits in Polish Large White nucleus herds. *J Anim Sci* 69, 91-98
- Keele JW, Johnson RK, Young LD, Socha TE (1988) Comparison of methods of predicting breeding values of swine. *J Anim Sci* 66, 3040-3048
- Kennedy BW, Schaeffer LR, Sorensen DA (1988) Genetic properties of animal models. *J Dairy Sci* 71 (suppl 2), 17-26
- Kovac M (1992) Derivative-free methods in covariance component estimation. PhD diss Univ Illinois, Urbana, Champaign IL, 141 p
- Kwon OS, Kim SH, Chung HW, Park YI (1986) A selection index for average daily gain and backfat thickness in pigs. *Korean J Anim Sci* 28, 635-640
- Long T, Brandt H, Hammond K (1990) Breeding value prediction with the animal model for pigs. In: *4th World Congr Genet Appli Livestock Prod*. Edinburgh, UK, 23-27 July 1990, vol XV, 465-468
- Lundeheim N, Johansson K, Andersson K (1980) Estimated phenotypic and genetic parameters based on data from the Swedish pig progeny testing stations. *Acta Agric Scand* 30, 183-188
- Malmfors B, Nilsson R (1979) Meat quality traits in Swedish Landrace and Yorkshire pigs with special emphasis on genetics. *Acta Agric Scand* 21(supp), 81-90
- Merks JWM (1987) Genotype \times environment interactions in pig breeding programmes. II. Environmental effects and genetic parameters in central test. *Livest Prod Sci* 16, 215-228
- Monin G (1983) Influence des conditions de production et d'abattage sur les qualités technologiques et organoleptiques des viandes de porc. In: *15^e Journées Rech Porcine en France*. Paris, 2-3 February 1983, Institut Technique du Porc, Paris, 151-176
- Numerical Algorithms Group (1990) *The NAG Fortran Library Manual-Mark 14*. NAG Ltd, Oxford, UK
- Ollivier L (1970) L'épreuve de la descendance chez le porc Large White français de 1953 à 1966. I. Analyse de la variation. *Ann Génét Sél Anim* 2, 311-324
- Ollivier L (1983) Dix ans d'une expérience de sélection individuelle sur des verrats utilisés en insémination artificielle. II. Paramètres génétiques estimés. *Genet Sel Evol* 15, 99-118
- Ollivier L, Derrien A, Molénat M (1980) Paramètres génétiques des verrats Large White et Landrace Français soumis au contrôle individuel de 1969 à 1978. Analyse préliminaire. *Techni-Porc* 3(1), 7-12

- Ollivier L, Derrien A, Molénat M (1981) Paramètres génétiques des femelles Large White et Landrace Français du contrôle de descendance sur la période 1970–1978. *In: 13^e Journées Rech Porcine en France*. Paris, 4–5 February 1981, Institut Technique du Porc, Paris, 293–298
- Patterson HD, Thompson R (1971) Recovery of inter-block information when block sizes are unequal. *Biometrika* 58, 545–554
- Press WH, Flannery BP (1986) *Numerical recipes*. Cambridge Univ Press, Cambridge, UK
- Robinson GK (1991) That BLUP is a good thing: the estimation of random effects. *Stat Sci* 6(1), 15–51
- Roehe R, Krieter J, Kalm E (1990) Efficiency of selection in a closed nucleus herd of pigs using an animal model – a simulation study. *In: 4th World Congr Genet Appl Livestock Prod*. Edinburgh, UK, 23–27 July 1990, vol XV, 469–472
- San Cristobal M (1992) Méthodes d'inférence statistique en modélisation de la variance. Application en génétique quantitative. Doctoral thesis, Univ Paul Sabatier, Toulouse, France, 228 p
- Savoie Y, Minvielle F (1988) Etude sur les porcs de race contrôlés en ferme au Québec. 2. Estimation des paramètres génétiques et phénotypiques. *Can J Anim Sci* 68, 1063–1068
- Schwörer D, Morel P, Rebsamen A (1987) Selection for intramuscular fat in pigs. Results of investigation in Switzerland. *Tierzuchter* 39, 392–394
- Searle SR, Casella G, McCulloch CE (1992) *Variance Components*. John Wiley and Sons, NY
- Sellier P (1988) Rapport général. Aspects génétiques des qualités organoleptiques et technologiques des viandes de porc. *In: 20^e Journées Rech Porcine en France*. Paris, 2–4 February 1988, Institut Technique du Porc, Paris, 227–242
- Sellier P, Guéblez R, Laloë D, Runavot JP, Ollivier L (1985) Relations génétiques entre le contrôle individuel en station et le contrôle en ferme chez le porc. *In: 17^e Journées Rech Porcine en France*. Paris, 30 January–1 February 1985, Institut Technique du Porc, Paris, 87–94
- Sorensen DA (1988) Effect of selection index *versus* mixed model methods of prediction of breeding values on response to selection in a simulated pig population. *Livest Prod Sci* 20, 135–148
- Sorensen DA, Vernessen AH (1991) Large scale selection for number of born piglets using an animal model. *In: Commission on Animal Genetics: 42th Annu Meet Eur Assoc Anim Prod*. Berlin, Germany, September 1991
- Tibau i Font J, Ollivier L (1984) La sélection en station chez le porc. *Bull Tech Dép Génét Anim No 37*. INRA, Versailles, 69 p
- Van Hofstraeten W, Vandepitte W (1988) Evaluation génétique de porcs reproducteurs de la race L. B. sur la base de données des stations de sélection. 2. Détermination de la valeur d'élevage au moyen d'un "multiple trait-animal model". *Rev Agric* 41, 913–921
- Van Steenbergen EJ, Kanis E, Van der Steen HAM (1990) Genetic parameters of fattening performance and exterior traits of boars tested in central stations. *Livest Prod Sci* 24, 65–82

Wray N (1989) Consequences of selection in closed population with particular reference to closed nucleus herds of pigs. PhD diss Univ Edinburgh, Edinburgh, UK, 177 p

Wyllie D, Morton JR, Owen JB (1979) Genetic aspects of voluntary food intake in the pig and their association with gain and food conversion ratio. *Anim Prod* 28, 381-390