

Genetic correlation estimations between artificial insemination sire performances and their progeny beef traits both measured in test stations

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Abstract – In France, beef traits of artificial insemination (AI) beef bulls are improved through the sequential selection for their own performances and for their male progeny performances, both being recorded in test stations. The efficiency of such programmes mainly depends on the genetic correlations between sire performances and progeny beef traits. Such correlations were independently estimated, using the multivariate REML (restricted maximum likelihood) method in a Limousin and a Charolais programme. In both breeds, high genetic correlations were observed between sires and progeny analogous morphology scores (from 0.64 to 0.82). Genetic correlations estimated between sires and progeny growth (from 0.41 to 0.70) were lower probably due to the difference of diet in central and progeny stations. Correlations between sire muscling scores and progeny skeletal frames (and *vice-versa*) were negative (from -0.05 to -0.58). The genetic correlations of sire traits with progeny dressing percentage (DP_p) and carcass fatness score (CF_p) were only low to moderate. These results show that the selection of bulls at the end of performance testing in test stations may be efficient in improving progeny growth and morphology. However, such a selection is insufficient in improving their dressing percentage and carcass composition.

genetic correlation / live and carcass traits / Charolais and Limousin breeds / selection efficiency

Résumé – **Corrélations génétiques estimées entre les aptitudes bouchères de taureaux d'insémination artificielle et celles de leurs fils contrôlés en stations.** En France, les aptitudes bouchères des races bovines allaitantes sont améliorées grâce à la sélection séquentielle de taureaux destinés à l'insémination artificielle (IA) (1) sur leur performances propres, (2) sur celles de leurs fils, toutes contrôlées

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en stations. L'efficacité de ces programmes est principalement liée aux corrélations génétiques entre les performances des pères et les caractères bouchers de leurs fils. De telles corrélations génétiques ont été estimées par la méthode du REML (restricted of maximum likelihood) multicaractère dans un programme de la race Limousine et un programme de la race Charolaise qui ont été analysés indépendamment. Dans les deux races, de fortes corrélations génétiques ont été estimées entre les caractères homologues de morphologie des pères et des fils (de 0,64 à 0,82). Les corrélations estimées entre les caractères de croissance des pères et des fils étaient plus faibles (de 0,41 à 0,70), probablement, en raison d'une différence de régime entre les stations de contrôle individuel et sur descendance. La conformation musculaire des pères et le développement squelettique des fils (et *vice-versa*) étaient négativement corrélés (de -0,05 à -0,58). Le rendement de carcasse (DP_p) et la note de gras interne (CF_p) des fils n'étaient que faiblement à modérément corrélés avec les caractères sélectionnés des pères. Ces résultats montrent que la sélection des pères est efficace pour améliorer les caractères de croissance et de morphologie mais qu'elle reste insuffisante pour améliorer le rendement et la composition de la carcasse.

corrélation génétique / caractères en vifs et d'abattage / races Charolaise et Limousine / efficacité de la sélection

1. INTRODUCTION

In France, bulls tested in central test stations have to be progeny tested in order to obtain accurate estimates of breeding values required for artificial insemination (AI) authorisation. Progeny tests are also done on test stations. Since only a limited number of bulls can be progeny tested simultaneously (8-13 bulls on the average per year and per station), the selection differential and, therefore, the expected genetic progress at the end of the progeny test cannot be of great magnitude. Part of the superiority of beef traits of tested bulls has to be acquired before progeny testing.

Performance testing in central test stations allows one to measure post-weaning beef production ability of a large number of candidates. In spite of the low accuracy of the bull breeding values estimated at the end of the bulls' own performance tests, a significant differential of selection can be obtained [11]. The expected genetic superiority of bulls is acquired if genetic correlations between the bull selected traits and their progeny traits, which are intended to be improved, are high enough.

The aim of this paper was to estimate the genetic correlations between sire traits and their progeny traits in order to ascertain the efficiency of sire selection in improving beef traits of economic importance.

Such genetic correlations have already been estimated in the French Charolais breed [13] using the REML (Restricted Maximum Likelihood) method for two trait analyses (a sire trait and a progeny trait).

These estimates need to be reconsidered for different reasons. More recent information on the Charolais selection programme is now available and, such information exists for the Limousin selection programme studied here. Variance component estimations can be obtained with more suitable methods such as the multivariate REML method. Furthermore, the literature about such genetic correlations concerning beef cattle is scarce.

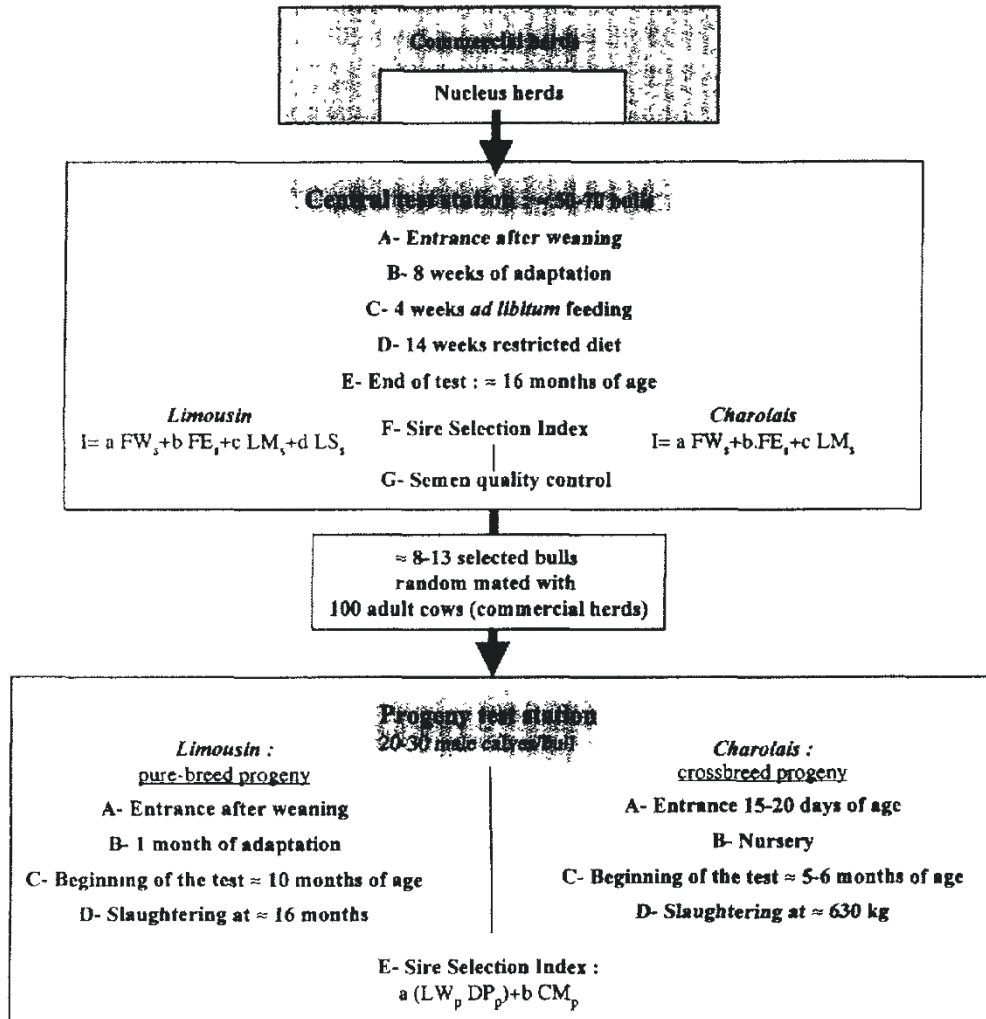


Figure 1. Testing procedures

2. MATERIALS AND METHODS

2.1. The testing procedures of the French AI programmes (Fig. 1)

Each year, new potential AI bulls in nucleus herds were bought at weaning by AI co-operatives and gathered in central test stations (on average 50 to 70 per year). Two or three groups of contemporary calves (born within a 6-week period) were then tested during a fixed period up to approximately 16 months of age. Performance testing started after 8 weeks of adaptation to testing conditions. During the first 4 test weeks, the bulls were fed *ad libitum* and growth potential was recorded. Then, feed efficiency was individually recorded during the last 14 test weeks. During this latter period, the amount of food

distributed per bull was adjusted weekly in order to obtain an average daily gain of $1300 \text{ g} \cdot \text{d}^{-1}$ in the Limousin breed and $1500 \text{ g} \cdot \text{d}^{-1}$ in the Charolais breed. The whole test diet was composed of highly digestible and not cumbersome whole grain pellets. Live weight measurements were made every 28 days during the tests. At the end of these tests, a sire selection index was calculated. Performance traits combined in this index depended on whether AI bulls were predominantly used for terminal crossbreeding or for pure-breeding. These traits were final weight, feed efficiency and muscle morphology for selecting terminal crossbreeding AI bulls. Skeletal frame score was added when AI bulls were used for pure-breeding [2]. Both programmes exist for each of the specialised beef breeds in France. The semen quality of selected bulls was assessed before progeny testing. This selection was not a strict truncation because some sires with high indexes were eliminated either for bad semen quality or other defects [11].

Selected bulls (on average, 8 to 13 per year) were randomly mated to about 100 adult cows in commercial herds. Three reference bulls were used simultaneously. About 20 to 30 male calves per tested and per reference sire were bought and set in test stations either at 15–20 days (crossbred) or at 6–7 months (pure-bred) of age. Management in stations was similar to management in usual commercial fattening units. Crossbred calves were raised in a nursery until the beginning of performance testing (5–6 months). Performance tests of the pure-bred calves started after 1 month of adaptation. At the beginning of the performance tests, calves were gathered in age-contemporary-groups (there was a maximum variation of 1 month). During the test period, calves were generally intensively fattened with corn silage distributed *ad libitum* and supplemented with protein like in usual commercial fattening units. Live weight measurements were made monthly during the test period. Young bulls were slaughtered under uniform conditions at a fixed age or fixed weight depending on the selection programme. Carcass traits were recorded. In each breed and each progeny test station, different year batches were genetically connected through the three national reference sires [2].

2.2. Animals considered

Genetic correlations between sire and progeny traits were estimated for performances recorded in central and progeny testing stations respectively using two data sets. In each specialised beef breed in France, both pure-bred and crossbred progeny tests exist. In the present analysis two programmes were considered separately: one Limousin and one Charolais. Limousin bulls were progeny tested on pure-bred young bulls slaughtered at the fixed age of 16 months and Charolais bulls were progeny tested on crossbred young bulls (Normand and Friesian dams) slaughtered at a fixed weight of 600 to 650 kg depending on the year.

The characteristics of the populations are given in Table I.

In the Limousin programme, 4532 pure-bred young bulls were controlled in progeny test stations for 11 consecutive years. These young bulls were sired by 131 bulls. Among these sires, 113 were previously performance tested

Table I. Population characteristics

	Limousin	Charolais Crosses
Nb of sires in CTS	587	2 265
Nb of sires progeny tested in PTS	131	145
Nb of sires progeny tested in PTS previously tested in CTS	113 (86%)	132 (91%)
Breed type of young bulls used for PTS	pure-breed	crossbreed
Breed of dams	Limousin	Normand or Friesan
Nb of young bulls	4 532	3 519
Nb of consecutive years of test in CTS	14	17
Nb of consecutive years of test in PTS	11	12

CTS Central Test Station. PTS Progeny Test Station

in a central station and selected. A total of 587 bulls were tested in the central test station over 14 consecutive years.

In the Charolais programme, 3 519 crossbred young bulls were controlled in a progeny test station for 12 consecutive years. These young bulls were sired by 145 bulls. Among these sires, 130 were previously selected out of 680 bulls performance tested in two central stations for 15 years. To get a better accuracy of the genetic values of the bulls in central test stations, 1 585 bulls that were tested in two other central test stations were included in the analysis since they were genetically related to the previous ones. Moreover, two out of these additional sires were also progeny tested on crossbred young bulls in the Charolais programme. Consequently in the Charolais programme, 132 sires out of that were 145 ones progeny tested, were previously performance tested in central test stations.

2.3. Recorded performances

Owing to the strict procedures and the restricted number of animals in the central test stations, many traits concerning growth, conformation and feed intake were accurately recorded. Both, live and slaughter performances of progeny were recorded in progeny test stations.

2.3.1. Performances recorded in central test stations (subscript "s")

The sire performances analysed in this study were:

- *Growth traits*. Average Daily Gain during the test period (ADG_s), Initial Weight (IW_s) and Final live Weight (FW_s);
- *Feed Intake*: Feed Efficiency (FE_s) defined as the difference between the predicted feed intake (function of live weight and weight gain) and the observed one;
- *Morphology scores*. Live Muscling (LM_s) and Live Skeletal frame (LS_s) scores

2.3.2. Performances recorded in progeny test stations (subscript "p")

As progeny young bulls were slaughtered, live and carcass performances became available. The beef traits analysed in this study were.

- *Growth traits.* Average Daily Gain during the fattening period (ADG_p), Initial Weight (IW_p) and Live Weight (LW_p) adjusted to 300 and 480 days respectively in the Limousin progeny and to 163 and 450 days in the Charolais crossbred progeny, by interpolation from the two nearest weights,
- *Slaughter yield:* Dressing Percentage (DP_p) defined as the ratio of hot carcass weight to final live weight;
- *Morphology scores* Live Muscling (LM_p), Carcass Muscling (CM_p) and Live Skeletal frame score (LS_p),
- *Fat score.* Carcass Fatness score (CF_p)

A very limited number of experienced technicians in each station provided the scores at the very end of the test period ($LM_{s\text{ and }p}$, $LS_{s\text{ and }p}$) and at slaughter (CM_p , CF_p)

2.4. Statistical models and methods

In order to estimate the genetic correlation between sire performances and progeny traits, multitrait models have to be used, combining performances measured on both bulls and their progeny. The variance-covariance components of these models were used to compute the relevant genetic parameters among bull performances, progeny traits and between both. The present study was focused on estimating correlations between bull performances and progeny traits. Genetic parameters among progeny traits were already presented in Fouilloux *et al.* [11] and are not reported in the present study. Additionally, we showed that prior selection of bulls (before entering the central test station and at the end of the bulls' own performance tests) did not significantly alter genetic parameters of progeny traits. The genetic parameters of sire traits were obtained, but are not reported here.

2.4.1. Models

After a preliminary analysis of variance to test for fixed effects (General Linear Model, SAS[®]), we used the following models:

Performances recorded in the central test stations

In both breeds, bull performances were analysed with an animal model: animal random effect (a) and the fixed age-group effect (cont). Initial weight was regressed on initial age. Feed efficiency, live muscling and skeletal frame scores were regressed on final age (βAge). In the Charolais breed, a pre-test environment (pretest) fixed effect was added (pretest: specific feeding management in the herd of origin or not):

$$\begin{aligned} \text{Ch } y_i &= \text{cont}_i + \text{pretest}_i + \beta\text{Age}_i + a_i + e_i \\ \text{Lim } y_i &= \text{cont}_i + \beta\text{Age}_i + a_i + e_i \end{aligned}$$

where y_i is the performance and e_i , the residual random effect of the i th bull.

Performances recorded in the progeny test stations

In both breeds, progeny performances were analysed with a sire model (s). The main fixed effects were: calving parity of the dam (calv: 2, 3, 4, 5 and over), region of origin (orig) and age-contemporary group (cont) of the male calves. Other fixed effects were included in the Limousin model, a management system until weaning (manag: indoor or outdoor weaned calves), in the Charolais model: breed of the dam (breed: Holstein-Friesian or Normand) and health status individually recorded in the nursery (pulm and diges: occurrence or absence of pulmonary or digestive troubles). In both breeds, average daily gain was regressed on initial age (βCov). Muscling (LM_p , CM_p), skeletal (LS_p) and fatness (LF_p , CF_p) scores were regressed on final age in the Limousin breed (βAge) and on final weight in the Charolais breed (βWeight).

$$\text{Ch } y_{ij} = \text{cont}_{ij} + \text{calv}_{ij} + \text{orig}_{ij} + \text{breed}_{ij} + \text{pulm}_{ij} + \text{diges}_{ij} \\ + \beta\text{Weight}_{ij} + s_i + e_i$$

$$\text{Lim } y_{ij} = \text{cont}_{ij} + \text{calv}_{ij} + \text{orig}_{ij} + \text{manag}_{ij} + \beta\text{Age}_{ij} + s_i + e_i$$

where y_{ij} is the performance of the j th male progeny of the i th sire.

2.4.2. Methods

The statistical analyses were conducted separately in both breeds. The general statistics (mean, standard error, number of tested young bulls) were calculated using SAS procedures.

The genetic parameters were estimated applying the Restricted Maximum Likelihood (REML) method. The analyses combined bull and progeny traits, systematically including the 3 or 4 bull traits included in the sire selection index at the end of the bulls own performance test (FW_s , FE_s and LM_s , in the Charolais programme, plus LS_s , in the Limousin programme). Two generations of ancestors of the sires were considered.

Estimates of variance components were computed using the VCE3.2 package developed by Neumaier and Groeneveld [19].

For each trait, the general statistics are given in Tables II (bull traits) and III (progeny traits). The genetic correlation coefficients are reported in Table IV.

3. RESULTS AND DISCUSSION**3.1. Means and phenotypic variability**

Means and phenotypic variability among progeny traits have already been described in Foulloux *et al.* [11].

In the Limousin central station, tests began 1 month earlier and on 99 kg lighter animals than in the Charolais station. In both programmes, the variability of the initial age was very low ($\text{CV} = 3.5\%$) and that of the initial weight was slightly higher ($\text{CV} \approx 6.5\%$). In the progeny test station, the variability of corresponding traits was higher ($\text{CV} \approx 11\%$ and 13% for initial

Table II. Sire traits – General statistics mean \pm standard deviation *

	Unit	Symbol	Limousin	Charolais
Initial Age	day		340 \pm 12	366 \pm 13
Initial Weight	kg	IW _s	446 \pm 27	545 \pm 40
<i>Ad libitum</i> Average Daily Gain	g d ⁻¹		1 313 \pm 273	1 494 \pm 414
<i>Limited</i> Average Daily Gain	g d ⁻¹		1 264 \pm 161	1 447 \pm 227
<i>Total</i> Average Daily Gain	g d ⁻¹	ADG _s	1 275 \pm 146	1 457 \pm 207
Final live Weight	kg	FW _s	611 \pm 36	730 \pm 49
Final Age	day		465 \pm 12	492 \pm 13
Feed Efficiency	kg d ⁻¹	FE _s	0 452 \pm 0 669	0 577 \pm 0 705
Live Muscling score	/100 pt	LM _s	62 7 \pm 8 0	71 6 \pm 8 8
Live Skeletal frame score	/100 pt	LS _s	61 5 \pm 7 7	70 0 \pm 8 3

* Within year batch standard deviation

Table III. Progeny traits – General statistics mean \pm standard deviation *

	Unit	Symbol	Limousin	Charolais Crosses
Initial Age	day		300 \pm 28	163 \pm 22
Initial Weight	kg	IW _p	349 \pm 54	210 \pm 24
Average Daily Gain	g d ⁻¹	ADG _p	1 395 \pm 179	1 191 \pm 117
Live Weight **	kg	LW _p	597 \pm 52	559 \pm 40
Slaughter Age	day		482 \pm 4	520 \pm 38
Slaughter Weight	kg		603 \pm 52	630 \pm 17
Dressing Percentage	%	DP _p	62 0 \pm 1 5	57 1 \pm 2 0
Live Muscling score	/100 pt	LM _p	62 9 \pm 9 3	63 0 \pm 8 8
Carcass Muscling score	/100 pt	CM _p	69 5 \pm 8 3	56 3 \pm 7 6
Live Skeletal frame score	/100 pt	LS _p	59 3 \pm 8 8	63 7 \pm 5 7
Carcass internal Fatness score	/100 pt	CF _p	57 8 \pm 10 5	54 8 \pm 7 1

* Within year batch standard deviation

** Adjusted to 480 and 450 days in the Limousin and the Charolais programme respectively

age and weight, respectively) In the Limousin programme, even though bulls entering the station were only 40 days older than their progenies, they were 100 kg heavier Bulls were chosen from nucleus herds whereas their progeny were bought from commercial herds. Such an observation could not be made for the Charolais programme since progeny tests were done on crossbred young bulls and began much earlier

In both central test stations, the standard deviation of final age remained equal to the standard deviation of initial age (12 and 13 days in the Limousin and the Charolais programme respectively) since the length of the test period was fixed at 18 weeks

In both programmes, the average daily gains over the *ad libitum* feeding period were slightly higher than the average daily gain during the entire test period (1 313 *versus* 1 275 g d⁻¹ in the Limousin programme and 1 494 *versus*

1 457 g d⁻¹ in the Charolais programme) The variability of average daily gain over the *ad libitum* feeding period was very high (CV = 21% and 28% in the Limousin and Charolais programme respectively) Such a feeding management enhanced the potential differences of the bulls' growth

In the Charolais programme, the average daily gain (ADG) of bulls over the entire test period was higher than the ADG measured on progeny (1 457 g d⁻¹ versus 1 191 g d⁻¹) This might be principally due to the difference of breed type (pure-bred versus crossbred) On the contrary, in the Limousin programme, the ADG of bulls over the entire test period was lower than the ADG measured on progeny (1 275 g d⁻¹ versus 1 395 g d⁻¹) This might be due to a limited growth rate during the limited feeding period in the central station (expected ADG 1 300 g d⁻¹, observed ADG *ad lib* 1 264 g d⁻¹) whereas progeny were fed *ad libitum*

The variability of morphology scores was relatively high with an average coefficient of variation of 12% for bull traits, similar to the corresponding traits of progeny

In both programmes, the average feed efficiency was higher than zero (FE mean = 450 and 580 g d⁻¹ in the Limousin and Charolais programme, respectively), showing that the real feed intakes of the bulls were generally lower than the expected ones The standard deviation of this feed efficiency criteria was around 700 g d⁻¹ in both breeds, which was around 7% of the actual mean feed intake

3.2. Genetic correlation coefficients (Tab. IV)

3.2.1. Genetic correlations between sire growth traits and:

Their progeny growth traits

In both breeds, the genetic correlations between average daily gain or live weight of sires and progenies were only moderately positive from 0.41 to 0.70 Correlations between analogous growth traits were lower in the Charolais programme (0.41 and 0.47 for average daily gain and live weight respectively) than in the Limousin programme (0.66 and 0.70, respectively). Differences of management in central and progeny test stations might explain why these genetic correlations were lower than unity Differences in feeding might influence bull physiology and then, growth expression In the Charolais programme, bulls and their progeny were of different breed types (crossbred progeny). Moreover, in that programme, tests in the central station began at about 366 days of age and ended at a fixed age whereas progeny tests began at about 163 days of age and ended at a fixed weight.

Some estimates of genetic correlations between dairy or dual-purpose bulls and progeny traits were presented during the EAAP (European Association of Animal Production) congress in Wageningen (Netherlands, 1987) and appear in other publications These estimates vary widely As suggested by Baker *et al.* [7] or Andersen [1], genetic parameters depend on many factors such as breed, definition of growth traits, pretest environment, starting-age of performance testing, management of the tested animal, feeding system, and age

Table IV. Genetic correlations (\pm standard error) between the sires and the progeny traits

		Progeny traits							
		ADG _p	IW _p	LW _p	DP _p	LM _p	CM _p	LS _p	CF _p
Sire traits	ADG _s	0.66 \pm 0.09	0.35 \pm 0.13	0.61 \pm 0.08	0.27 \pm 0.14	0.20 \pm 0.05	0.13 \pm 0.14	0.54 \pm 0.06	-0.47 \pm 0.17
		0.41 \pm 0.08	0.52 \pm 0.12	0.47 \pm 0.06	0.06 \pm 0.13	-0.12 \pm 0.07	-0.04 \pm 0.08	0.20 \pm 0.07	-0.18 \pm 0.05
	IW _s	0.20 \pm 0.07	0.61 \pm 0.08	0.48 \pm 0.07	-0.06 \pm 0.03	0.26 \pm 0.07	0.24 \pm 0.06	0.15 \pm 0.08	0.02 \pm 0.03
		0.64 \pm 0.07	0.57 \pm 0.14	0.51 \pm 0.06	0.03 \pm 0.12	0.19 \pm 0.05	0.15 \pm 0.10	0.12 \pm 0.10	0.26 \pm 0.11
	FW _s	0.41 \pm 0.10	0.77 \pm 0.09	0.70 \pm 0.09	0.04 \pm 0.08	0.34 \pm 0.06	0.36 \pm 0.09	0.32 \pm 0.08	-0.12 \pm 0.08
		0.58 \pm 0.11	0.65 \pm 0.11	0.47 \pm 0.08	0.13 \pm 0.12	0.05 \pm 0.07	0.10 \pm 0.11	0.13 \pm 0.10	0.11 \pm 0.11
	FE _s	0.34 \pm 0.13	0.09 \pm 0.15	0.26 \pm 0.13	0.17 \pm 0.15	0.11 \pm 0.07	0.07 \pm 0.11	0.17 \pm 0.09	-0.27 \pm 0.09
		0.37 \pm 0.07	0.16 \pm 0.11	0.27 \pm 0.07	0.18 \pm 0.09	-0.05 \pm 0.05	0.06 \pm 0.08	0.00 \pm 0.06	0.11 \pm 0.07
	LM _s	-0.13 \pm 0.11	0.21 \pm 0.11	0.06 \pm 0.10	0.28 \pm 0.10	0.82 \pm 0.05	0.64 \pm 0.10	-0.34 \pm 0.07	-0.11 \pm 0.10
		-0.17 \pm 0.11	0.03 \pm 0.15	-0.23 \pm 0.07	0.59 \pm 0.10	0.66 \pm 0.07	0.79 \pm 0.07	-0.05 \pm 0.08	-0.19 \pm 0.09
	LS _s	-0.01 \pm 0.12	0.54 \pm 0.11	0.31 \pm 0.12	-0.07 \pm 0.11	-0.48 \pm 0.07	-0.58 \pm 0.10	0.77 \pm 0.05	-0.05 \pm 0.11
		0.59 \pm 0.15	0.15 \pm 0.12	0.48 \pm 0.06	-0.08 \pm 0.09	-0.50 \pm 0.07	-0.31 \pm 0.07	0.70 \pm 0.08	0.23 \pm 0.06

ADG Average Daily Gain, IW age-adjusted Initial Weight, LW age-adjusted Live Weight, FW Final Weight, DP Dressing Percentage, LM Live Muscling score, CM Carcass Muscling score, LS Live Skeletal frame score, CF Carcass internal Fatness score, FE Feed Efficiency Upper Line Limousine, Lower Line Charolais "s" subscript Sire trait, "p" subscript Progeny trait

interval Chavaz [9] observed that the genetic correlation between average daily gain of Brown Swiss bulls and their progeny carcass weight increased with the percentage of progeny Brown Swiss blood. Moreover, in the analysis presented in Wageningen, while bulls were usually tested in central test stations, different kinds of progeny tests were done: station testing, contract fattening of herds or field conditions, and testing with pure-bred or crossbred progenies. In dairy and dual-purpose breeds, bulls may be gathered early in central test stations whereas in beef breeds, testing of bulls starts only after weaning (at 7 months of age). Consequently, beef bull performances at the beginning of the tests are greatly influenced by the herd of origin [15, 26].

The estimations of genetic correlations between beef bulls and progeny traits are scarce. Some authors tried to approach these parameters using different methods and models. Hence Wilton and McWhir [27] estimated product-moment correlations between the individual growth performances of sires tested in central test stations and the predicted difference of their progeny growth in herds on performance recording. These correlations are low but close to their expectation, approximated as the average of the expectation of the correlation for each sire: from 0.16 between the ADG relative to their contemporary group of sires and the post-weaning gain of the progeny, to 0.30, between sire and progeny yearling weight. The authors therefore deduced that sire performance tests in central stations result in moderately accurate estimates of subsequent progeny performance. Furthermore, under divergent selection of bulls, Baker *et al* [6] also found very low correlations (0.15) between the sires' age-adjusted final weight and their 550-day live weight progeny difference. These authors concluded that, in New Zealand, sire selection at the end of central performance tests is not efficient. On the contrary, in a divergent selection experiment in the Charolais breed, Renand *et al* [22] estimated high genetic correlations ($r_g = 0.83$ for final weight and 0.91 for average daily gain) showing that sire selection on growth performances may improve their progeny growth rate.

Their progeny morphology scores

In the Limousin programme genetic correlations between sire growth traits and progeny muscling scores (LM_p and CM_p) or live skeletal frame score (LS_p) were moderately positive (from 0.13 to 0.54). The corresponding correlations were low in the Charolais breed: from -0.12 to 0.20. Consequently, ignoring other selected traits, it could be expected that sire selection on final weight might improve the morphology of Limousin progenies, but not that of the Charolais progenies.

In the literature, estimated correlations between sire growth and their progeny morphology depended on breed and the traits analysed: from -0.41 between sire average daily gain (ADG_s) and estimated thigh volume in a Brown Swiss programme [9] to 0.59 between ADG_s and carcass fleshiness of veal progeny in the Dutch Red and White breed [10]. Most of them were moderately positive [1, 4, 21, 23].

3.2.2. Genetic correlations between sire morphology traits and:

Their progeny morphology scores

In both breeds, sire live muscling score (LM_s) was highly genetically correlated ($r_g > 0.60$) with progeny live and carcass muscling scores (LM_p and CM_p). Similarly, the sire live skeletal frame score (LS_s) was highly genetically correlated ($r_g > 0.70$) with progeny live skeletal frame score (LS_p). On the contrary, genetic correlations between either sire muscling score and progeny skeletal frame score or sire skeletal frame score and progeny muscling scores were all negative: most of them were between -0.31 and -0.58 .

In the Limousin programme, LM_s and LS_s were both included in the selection index. Direct selection of sires considering LM_s might influence progeny muscle scores but, due to the negative correlations between LM_s and LS_p , it might damage LS_p . On the contrary, direct selection of sires considering LS_s might influence LS_p but might damage LM_p or CM_p .

In the Charolais breed, LS_s was not included in the sire selection index and LM_s was independent of LS_s ($r_g = -0.05$). Ignoring other selected traits, sire selection considering LM_s might influence progeny muscularity (LM_p and CM_p) without modifying their skeletal frame (LS_p).

In the literature, genetic correlations between sire and progeny morphology traits are scarce. Dijkstra *et al* [10] and Oldenbroek *et al* [21] estimated low to moderate positive correlations between the live fleshiness of sires recorded at 365 days of age in central test stations and the carcass fleshiness of their progeny in fattening units (0.18 and 0.54: veal production, 0.37 and 0.38: beef production). These low correlations between analogous traits might be due to either the difference of maturity at recording between sires and their progeny or to the difference of management (test station *versus* fattening units). Averdunk *et al* [4] estimated negative (≈ -0.30) and null ($+0.04$) genetic correlations between sire height at wither at 365 days of age (frame size) and progeny conformation score measured in contract farms and under field conditions respectively. These authors also estimated positive correlations between the sires' chest girth, round circumference or tour spiral and their progeny conformation score in contract farms (from 0.39 to 0.65) or under field conditions (0.14 to 0.17).

Their progeny growth traits

In the Limousin programme, the live muscling score of sires (LM_s) was genetically independent of progeny live weight (LW_p , 0.06) and had a low and negative correlation to progeny average daily gain (ADG_p , -0.13). The sire live skeletal frame score (LS_s) was independent of ADG_p (-0.01) but moderately genetically correlated with progeny weight (LW_p , 0.31). According to the genetic correlations between LS_s and LS_p (0.77) and between LS_p and progeny weights ($r_g > 0.60$ [11]), it could be expected that the selection of Limousin sires, considering their skeletal frames, might modify the skeletal growth of their progenies, and, therefore, progeny weight.

In the Charolais programme, the correlation between LM_s and progeny growth rate was low and negative (-0.17 and -0.23 with ADG_p and LW_p

respectively) Progeny growth may be slightly damaged through the selection of sires on LM_s . LS_s was positively correlated with progeny growth rate (0.59 and 0.48 with ADG_p and LW_p respectively). LS_s was not included in the selection index of Charolais sires.

In the literature, the genetic correlations between muscularity of sires and the growth of their offspring varied widely from -0.74 between the LM_s of sires at 365 days of age and their progeny carcass weight (veal production) [10] to 0.51 between the sire round circumference and the carcass weight or the net gain of their progeny under field conditions [4]. The genetic correlations between sire frame traits and their progeny growth traits are usually positive, ranging between 0.07 (sire height at withers at 12 months with slaughter weight) [12] and 0.77 (sire pelvic height with veal or beef carcass weight) [10]

3.2.3. Genetic correlations between the sire feed efficiency (FE_s) and progeny traits

In both programmes, genetic correlations between the sire feed efficiency (FE_s) and their progeny traits showed the same tendencies

FE_s was moderately and positively correlated with their offspring growth rate (LW_p and ADG_p) ($r_g \approx 0.30$). In a Charolais experimental programme, Renand *et al* [22] found more favourable genetic correlations between FE_s and progeny growth traits (0.45, 0.46 and 0.65 with LW_p , carcass muscle weight and ADG_p , respectively). These authors used the residual feed intake that was the opposite of feed efficiency. They also estimated a genetic correlation of 0.61 between the sire and their progeny feed efficiency (FE_s and FE_p). In the present analysis, during the progeny test period, young bulls were fattened with corn silage distributed *ad libitum*. Consequently, two principal components governed growth capacity: feed intake and feed efficiency (ability to transform ingested nutriment) In central test stations, sires were fed with a whole grain pellet diet. Feed efficiency was therefore, the principal component of growth rate. In progeny test stations, food was more cumbersome and, therefore both feed intake and feed efficiency were involved. The estimated genetic correlation showed that selecting sires according to their FE_s should primarily improve their progeny FE_p, and also, to a lower degree, their progeny growth rate.

FE_s was almost independent of progeny muscling and skeletal frame scores. Almost no effect of sire selection on FE_s was expected on progeny morphology

In the literature, many different definitions of feed efficiency exist such as feed intake (FI, [3,24]), metabolisable energy intake [20], residual feed intake [3,22], feed conversion ratio (feed intake/gain) [20], the Kleiber ratio (= $ADG / \text{mass}^{0.75}$) [16] used in South Africa, gross feed efficiency [20], etc. In most of these publications, genetic correlations between feed intake and growth are positive, situated between 0.59 [24] and 0.95 [20]. No genetic correlation between these traits and conformation traits was found.

3.2.4. Genetic correlations between sire performances and their progeny Dressing Percentage (DP_p)

In both breeds, the progeny dressing percentage (DP_p) was lowly related to sire skeletal development score (LS_s $r_g \approx 0.07$), sire final weight (FW_s)

and average daily gain (ADG_s) (r_g from 0.04 to +0.27) or feed efficiency (FE_s, $r_g \approx 0.17$). Hence, DP_p was little influenced by selection of sires on their FW_s, FE_s and, in the Limousin programme, LS_s. On the contrary, DP_p was positively genetically correlated to the sire live muscling score (LM_s) especially in the Charolais programme ($r_g = 0.59$ versus 0.28 in the Limousin breed). These coefficients were close to the genetic correlations between live muscling score (LM_p) and DP_p of progeny estimated by Fouilloux *et al.* [11] moderate (0.22) in the Limousin, and high (0.61) in the Charolais programme. Consequently, sire selection on LM_s may improve DP_p *via* its effect on progeny carcass muscling score especially in the Charolais programme.

In the literature, genetic correlations between DP_p and sire growth traits were usually low from -0.12 [4] to 0.19 [12]. In the same way, genetic correlations between DP_p and the sire frame size varied from -0.23 [4] to 0.06 [12]. Correlations between DP_s and the sire measure of body circumference estimated by Averdunk *et al.* [4] range from -0.40 (progeny testing in contract herds) to 0.13 (progeny testing in test stations). Genetic correlations between DP_s and muscularity of sires were not found in the literature.

3.2.5. Genetic correlations between sire traits and their progeny carcass fat score (CF_p)

In the Limousin programme, a negative genetic correlation was estimated between progeny carcass fat score (CF_p) and sire average daily gain (ADG_s; $r_g = -0.47$). On the contrary, Fouilloux *et al.* [11] estimated a positive genetic correlation between CF_p and progeny average daily gain (ADG_p; $r_g = +0.38$).

In the Charolais programme, the genetic correlation between CF_p and ADG_s was also negative but to a lower degree ($r_g = -0.18$). Fouilloux *et al.* [11] estimated a positive genetic correlation between (CF_p) and ADG_p ($r_g = +0.17$).

These observations led to the conclusion that the faster a sire grows up, the leaner the progeny will be, while the faster its progeny grow up, the fatter the progeny will be.

Genetic correlations between CF_p and feed efficiency of the sire (FE_s) were negative, especially in the Limousin programme (-0.27 versus -0.11 in the Charolais programme).

No clear genetic correlations were found between sire final weight (FW_s) or morphology (LM_s, LS_s) and progeny carcass fatness (CF_p).

The present results showed that the selection of bulls on their own growth rate measured with a highly digestible and not cumbersome diet might principally improve their genetic ability to use nutrients for muscle growth since their progeny growth was higher and their progeny carcass leaner. The results obtained by Fouilloux *et al.* [11] with progenies fed corn silage *ad libitum* show that genetic improvement in the progeny station conditions might induce a correlated increase in carcass fatness. This discrepancy may be explained if we consider that growth rate measured in these latter conditions also depends on feed intake capacity and if that capacity is genetically related to increased fatness (Renand, personal communication).

In the literature the relation between growth, feed efficiency and carcass composition mainly depends on feed management as the composition of the

diet (digestibility) or the amount of food (restricted *versus ad libitum*) [5,8,14,17,18]. Breed type and age or weight at slaughter also influence that relation [5,8,17]. Analyses of the influence of management on the relationship between fatness and conformation are scarce. Nevertheless, management conditions might affect this relation.

In other studies, as in the present study, most of the estimated genetic correlations between progeny fatness traits and sire traits (morphology, growth) are low ($|r_g| < 0.30$) [4,10,12]. Solely Renand *et al.* [22] have estimated a moderate and negative genetic correlation between progeny carcass fat content and sire ADG ($r_g = -0.41$) and Dijkstra *et al.* [10], a highly positive correlation between progeny fat covering score and sire live muscling score ($r_g = 0.64$).

4. CONCLUSION

In spite of the difference of testing conditions in both central and progeny test stations (pre-test environment, feeding diet and regime), the genetic correlations estimated between sires and their progeny morphology scores were high whereas those for growth traits were only moderate (from 0.5 to 0.7). Andersen [1] suggested that genetic parameters are mainly influenced by breed, definition of the traits, tested animal management (test stations, field..., diet, age...) and other external factors. Our estimated genetic correlations suggested that different components of growth ability were favoured in the different stations. This could also explain the differences between genetic correlations estimated between progeny or sire growth traits and progeny carcass fatness scores. On the contrary, genetic correlations between sires and their progeny morphology scores were high (from 0.64 to 0.82), suggesting that such traits were less dependent of feeding conditions and constraints.

In both programmes, genetic selection of sires in central test stations should be efficient in improving progeny growth, muscle development and, in the Limousin breed, skeletal development. It should be noted that if the selection of the 12 best sires out of 50 for a trait with a heritability of 0.3 precedes the selection of the 6 best sires out of 12 based on the progeny performance with a heritability of 0.3 and a coefficient of determination of 0.6, then the total response to selection is increased from 40% (moderate genetic correlation between sire and progeny traits) to 100% (with very high genetic correlation). Progeny tests remain, however, necessary to improve dressing percentage and carcass composition that are lowly correlated to sire traits.

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