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The chemical composition of carcasses can be predicted from proxy traits in finishing male beef cattle: A meta-analysis

M. Al-Jammas, J. Agabriel, J. Vernet, I. Ortigues-Marty *

INRA, UMR1213 Herbivores, F-63122 Saint-Genès-Champanelle, France
Clermont Université, VetAgro Sup, UMR1213 Herbivores, BP 10448, F-63000, Clermont-Ferrand, France

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ABSTRACT

Management practices can contribute to improving carcass quality if carcass quality could be simply evaluated under a wide range of conditions. The objective of this study was to derive quantitative relationships between the most accurate (but laborious) measurements of carcass chemical composition and proxy traits easily obtainable at slaughter (yield grade, subcutaneous fat thickness, marbling, ribeye area and hot carcass weight) by meta-analysis. Data from 34 publications using male beef cattle were used to develop and validate the models. The breeds were characterized according to origin, rate of maturity, production purpose and frame size. The results indicated that the changes in carcass fat and protein can be predicted from the yield grade or subcutaneous fat thickness, and hot carcass weight, with prediction errors ranging between 9 and 12%. Including the breed characteristics in the models did not improve the fit. The relationships are applicable to group values of male beef cattle having light and fatty carcasses from early-maturing British breeds.

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1. Introduction

In cattle, carcass quality is an important criterion in the grid of payment to producers, with quality being defined by the adiposity and the muscularity of the slaughtered animals. However, the development of management practices that drive carcass quality has remained limited because of the methodological difficulty of evaluating carcass quality (Craigie et al., 2012). The evaluation of carcass quality has been approached by a number of different methods targeting different anatomical regions. We classified them as direct or indirect (Kempster, 1986). Direct methods determine the chemical or physical composition of either the entire carcass or a single side. Chemical analysis (Powell and Huffman, 1968) was found to be prevalent with American studies. Tissue dissection of the carcass was mainly performed in Europe with a focus on retail yield (Lunt et al., 1985) or tissue development (Robelin, 1986a). These direct methods may be considered as reference methods because they are the most accurate for determining carcass composition. They are, however, expensive, time consuming and unsuitable for wide-scale use. As a result, they have been progressively abandoned to the benefit of indirect methods.

Over the last several decades, indirect methods have been developed as proxy traits of carcass or meat quality. Proxy traits can be measured on specific anatomical regions. They can be easily and rapidly obtained; however, they vary greatly from one country to another (Polkinghorne and Thompson, 2010). In the European Union (E.U.), beef carcasses are classified according to their conformation and fatness. In other countries such as the U.S.A., marbling score (MAR), subcutaneous fat thickness (SFT), ribeye area (REA), yield (YG) and quality grade are usually evaluated.

Numerous published studies have addressed the influence of management factors on beef carcass quality (e.g., Ceconi, Ruiz-Moreno, DiLorenzo, DiCostanzo, and Crawford, 2015; Domingues et al., 2015; Krueger et al., 2010). However, they did not systematically report the same proxy traits, and it is not clear whether these proxy traits reflect the same changes in carcass composition as do the direct methods. This poses a difficulty when trying to combine results in a meta-analysis. A few studies established correlations between proxy traits and the chemical composition of the whole carcass using individual animal data (Delfa, Colomer-Rocher, and Teixeira, 1992; Indurain, Carr, Goñi, Insausti, and Beriain, 2009). Relationships were also derived between reference measurements and combinations of proxy traits of individual animal data (O'Mara et al., 1998). Those relationships were established under well-controlled but limited conditions, such as a given diet, breed (Costa, Valadares, Detmann, Marcondes, and Rotta, 2013) or a given sex (Crouse and Dikeman, 1974); consequently, they are not applicable to other conditions. Therefore, in isolation, these studies cannot test whether the relationships are robust across breeds (e.g., British vs Continental) and whether they are independent of the progress in genetic improvement. Overall, it remains unclear whether

* Corresponding author.
E-mail address: isabelle.ortigues@clermont.inra.fr (I. Ortigues-Marty).

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proxy traits are consistently related to carcass composition across different production systems and animal characteristics and for groups of animals.

Because allometric relationships exist within an animal breed or type, for instance between a specific adipose tissue (e. g., subcutaneous or intramuscular adipose tissue) and total carcass adipose tissue development (Tatum, Williams, and Bowling, 1986), we assumed that proxy traits are significantly related to carcass composition but that the relationship is significantly affected by animal characteristics. The purpose of the present study was to test using a meta-analysis on published data whether quantitative relationships between the reference measurements of carcass composition, defined for the purpose of this work as carcass fat and protein masses, and proxy traits could be obtained over a wide range of conditions. The potential confounding factors in these relationships were also explored, and the prediction potential of the models was evaluated using an independent database. The present work is strictly focused on the chemical composition of the bovine carcass and does not address tissue composition.

2. Materials and methods

Animal Care and Use Committee approval was not obtained for this study because the data were assembled from previously published studies.

2.1. Data sources and collection

Peer-reviewed publications were searched using Web of Science without a restriction on the years or on journals based on the following keywords: cattle, heifer, steer, bull or cow in combination with carcass traits, carcass characteristics, carcass quality or carcass composition. Additional studies were included by manual review of the reference list of the selected publications. To be eligible, the publications had to report results on reference measures of carcass chemical composition (protein or fat or both) in addition to at least one proxy trait (REA, Mar, SFT, YG) as defined further below. The publications were limited to *Bos taurus* and to male beef cattle because of the scarcity of data on *B. indicus*, dairy breeds and females.

The quantitative data extracted from the eligible publications (n = 34) as average group data are listed in Table 1. All eligible publications were dated before 2002 with the majority before 1990, and they were published in the same journal reflecting the prevalence of the chemical determination of the whole carcass in American studies. They were randomly assigned either to a development dataset for the development of models (70% of total publications) or to a validation dataset for an external validation of models (30% of publications) as recommended by Mucherino, Papajorgji, and Pardalos (2009). As a result, the development dataset was constituted from 24 publications (30 studies and 161 treatments), and the validation dataset was constituted from 10 publications (11 studies and 45 treatments). The selected publications did not systematically report all relevant data or express data in the same units. Hence, when possible, the missing data were recalculated from the results present in the publications, and the units were homogenized (see Supplementary Table S1).

2.2. Animal typology

We assumed that animal characteristics influenced the meta-analysis (McPhee, Oltjen, Famula, and Sainz, 2006). Hence, an animal typology was set up. The objective was to identify the most relevant animal characteristics to include in the meta-analysis to limit potential confounding effects. The typology aimed to address genetic progress, sex and breeds.

The genetic improvement of cattle breeds with regards to efficiency and production and the associated changes in carcass composition (Cundiff et al., 1993) was identified by the year of publication. Three arbitrary classes were defined: A1: <1980, A2: 1980-1990, and A3: >1990.

For the sex, the implant status was considered for its impact on performance and carcass quality (Bruns, Pritchard, and Boggs, 2005). Hence, the categories of sex were defined as follows: non-castrated males (M), castrated males (CM), implanted non-castrated males (IM), and implanted castrated males (ICM).

The breeds were characterized according to common criteria and not according to breed names because of the variety of breeds found in the retrieved publications. A whole range of breed characteristics was obtained from published reviews, web sites, or by the authors' expertise (for details see Supplementary Data S2 and Tables S2a and S2b). To identify the most relevant and independent breed characteristics for consideration in the meta-analysis, the correlations between all of these criteria were investigated by a multiple correspondence analysis and Chi-Square test for the qualitative factors (breed origin, purpose, maturity, frame size) and by a matrix of correlation and principal component analysis for the quantitative factors (adult male weight, female

Table 1
Description of data used in the meta-analysis: mean, standard deviation, range and median of variables for live animal and carcass characteristics, in the development and validation datasets.

Definition	Unit	Development dataset						Validation dataset						*P* value t-test
		Number[a]		Mean	SD	Min	Max	Median	Number[a]		Mean	SD	Min	Max	Median	
		n_e	n_m						n_e	n_m						
Days of trial	d	139	22	189.0	62.0	70.0	315.0	189.0	17	28	123.0	19.0	98.0	152.0	112.0	0.000
Initial body weight	kg	137	24	277.0	62.7	139.6	541.0	274.4	22	23	277.3	46.0	225.5	361.0	269.0	0.982
Slaughter body weight	kg	147	14	502.7	55.8	399.0	682.3	500.0	9	36	445.3	65.7	369.0	530.0	433.0	0.079
Average daily gain	kg/d	141	20	1.24	0.23	0.82	1.88	1.23	19	26	1.16	0.36	0.32	1.78	1.18	0.366
Hot carcass weight	kg	160	1	309.2	40.3	210.0	431.8	310.2	45	0	314.5	51.2	208.0	403.5	318.0	0.525
Cold carcass weight	kg	160	1	303.1	39.5	205.8	423.2	304.0	45	0	308.3	50.1	203.8	395.4	311.6	0.520
Dressing percentage	%	146	15	61.1	3.7	45.6	70.3	61.6	24	21	61.6	1.9	57.3	64.5	61.6	0.369
Carcass fat weight	kg	160	1	94.9	15.9	54.5	146.7	94.0	45	0	90.4	24.9	33.6	134.5	91.99	0.252
Carcass protein weight	kg	109	52	45.4	6.6	27.9	59.9	45.5	39	6	48.3	8.9	29.0	65.7	46.4	0.067
Carcass water weight	kg	109	52	156.1	23.2	98.6	211.8	159.0	38	7	161.9	26.3	115.1	205.2	160.7	0.262
Carcass fat concentration	%CCW	161	0	31.2	3.4	22.6	40.4	30.8	45	0	28.8	5.2	15.4	40.8	29.3	0.005
Carcass protein concentration	%CCW	110	51	14.9	1.4	11.3	20.4	14.9	39	6	15.9	2.3	12.6	23.1	15.6	0.019
Carcass water concentration	%CCW	110	51	51.2	3.4	39.5	58.9	51.9	38	7	52.6	3.3	45.0	59.4	52.0	0.025
USDA yield grade	1 to 5	142	19	3.0	0.5	1.7	4.7	3.0	32	13	2.9	0.63	1.2	4.3	3.0	0.177
Subcutaneous fat thickness	mm	149	12	12.1	3.1	4.5	21.0	12.2	45	0	11.8	4.1	2.2	21	11.8	0.670
Marbling score	10 points	126	35	4.0	0.7	2.1	6.1	4.0	41	4	3.8	0.6	2.4	4.7	3.9	0.136
Ribeye area	cm^2	152	9	77.5	6.7	62.6	96.1	76.6	39	6	77.6	10.6	57.4	98.5	75.3	0.963
Kidney, pelvic, and heart fat	%HCW	128	33	2.9	0.7	0.2	4.7	3.1	39	6	1.9	0.8	0.3	3.5	1.7	0.000

[a] Number of data (treatment). n_e: number of existing data, n_m: number of missing data.

adult weight, birth weight and height of the adult animal). Four classes of typology criteria were defined (Fig. 1), as follows: (i) the production purpose (dairy, beef and dual purpose); (ii) the maturity characteristics of the breed (early, intermediate, and late maturing); (iii) the breed's origin (British, Continental, composite, dairy); and (iv) the frame size (large, medium and small), which could also be defined from the weight and height of animals at birth and in mature adults (Dhuyvetter, 1995). Moreover, very high correlations were found (details not shown) between the classes of origin (British vs Continental), frame size (small vs large), and maturity (early vs late maturing), confirming previous knowledge (Littler and Wales, 2007). On those bases, the most relevant breed characteristics were identified as being (1) the production purpose and (2) the maturity characteristics. The latter is known to reflect the genetic potential of breeds for body tissue development (bone, muscle and fat) and the mature frame size in normal growth situations (Robelin, 1986a).

2.3. Meta-analysis

Meta-analyses were performed according to the heuristic method of Loncke et al. (2015) and Sauvant, Schmidely, Daudin, and St-Pierre (2008). All data were examined graphically at each step of the analysis.

2.3.1. Meta-design and coding of studies

The meta-design was described by descriptive statistics (mean, standard deviation, minimum, maximum, median, Student t-test, and ANOVA). The normality of the data (Shapiro and Wilk, 1965; Ghasemi and Zahediasl, 2012) and the independence between the covariates (i.e., between hot carcass weight (HCW) and each proxy trait as detailed below) were checked. The publications reporting more than 1 experimental study were separated into studies that were individually encoded as such.

2.3.2. Response and independent variables of the statistical models

The independent variables under focus were each of the proxy traits (REA, MAR, SFT, and YG), and the response variables were the carcass fat and carcass protein masses obtained by reference methods.

Three direct methods of determination of carcass composition were considered as reference methods. For each of these methods the chemical composition of the carcass was determined by the authors of the publications from 1) the Rib Dissection method based on the measured chemical composition of the 9th, 10th and 11th rib (Hankins and Howe, 1946); 2) the Specific Gravity method (Garrett and Hinman, 1969); and 3) a prediction method (Crouse, Dikeman, and Allen, 1974; Powell and Huffman, 1973) based on a combination of indirect measurements (the percentage of kidney, pelvis and heart fat (KPH), YG, quality grade, SFT, REA, HCW, MAR and Muscling). Each of these reference methods had been compared with a full carcass chemical analysis performed after carcass grinding (Crouse et al., 1974; Garrett and Hinman, 1969; Hankins and Howe, 1946; Powell and Huffman, 1973).

As for the proxy traits, the measurement of SFT and REA was on the 12th rib in most publications except for Murphy & Loerch (1994, 6, 7, 8th rib); Crawford, Anthony, and Harris (1978) and Rossi, Loerch, and Fluharty (2000) who did not define the rib number. The MAR was measured on the 12th rib but was expressed according to different scoring scales depending on the year of publication. The MAR scores were harmonized on a scale of 10 points (2 tracks, 3: slight, 4 small) according to USDA (1965). The YG was always estimated according to USDA (1965):

$$YG = 2.5 + (0.0984 \times SFT, mm) + (0.008378 \times HCW, kg) + (0.2 \times \%KPH) - (0.0496 \times REA, cm^2).$$

2.3.3. Selection of units and of the statistical model

The choice of unit for the response variables as well as the additional covariates to consider in the statistical models proved to be critical. A heuristic approach was applied to select the most relevant units and covariates. As indicated earlier, the masses of carcass fat and carcass protein were considered and were hence expressed in kilograms. A preliminary analysis had indicated that when the carcass fat and carcass protein are expressed as concentrations (Al-Jammas, Vernet, Agabriel, and Ortigues-Marty, 2014), the residuals of the models were significantly correlated with carcass weight (results not shown). A mass unit had also been recommended by Costa et al. (2013) to compare data from different breeds, ages and weights at slaughter and by Charles and Johnson (1976) to account for the large between-breed differences in carcass composition at a similar carcass weight. As a result, HCW was systematically included in the models as an independent variable. Residuals remained significantly affected by animal typology criteria. On those bases, within-study models in which animal typology criteria were considered as additional covariates were developed. Because of imbalanced data in the eligible publications when considering the typology criteria (production purpose × maturity characteristics × sex), each typology criterion was introduced separately in the models.

Relationships were then established from the development dataset according to a within-study variance–covariance model using Minitab software (Minitab® 16.2.4. 2013). The study effect was considered as fixed to account for the limited number of publications eligible for the meta-analysis (Sauvant et al., 2008) and to acknowledge and explore the influence of experimental conditions on the relationships (Loncke et al., 2015). Having the study effect fixed recognizes the non-random

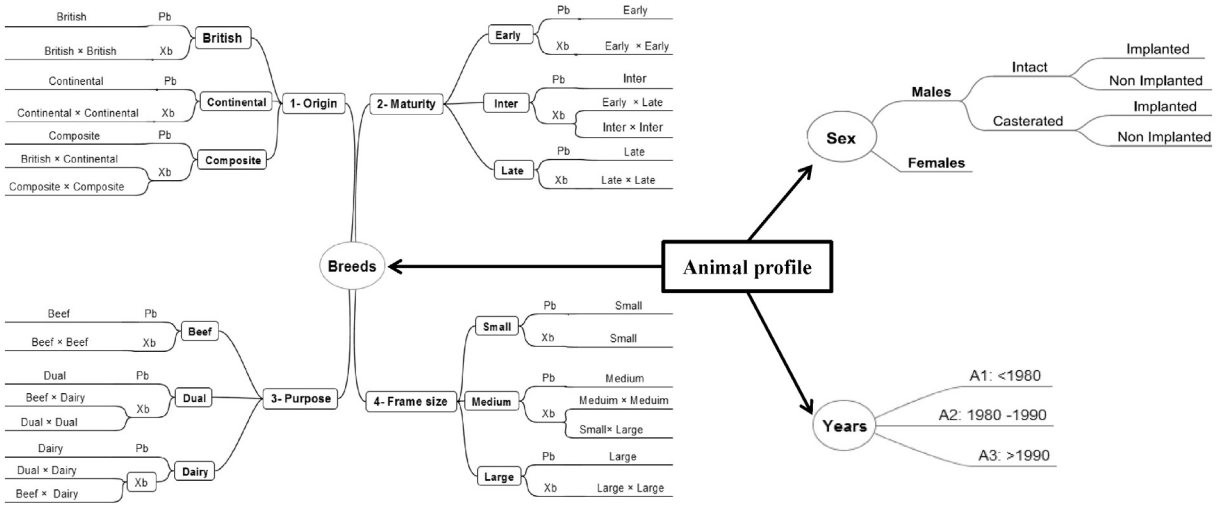


Fig. 1. Animal typology developed to characterize animals according to sex and breeds (Pb: Purebreds, Xb: Crossbreeds, Inter: Intermediate) in the development and validation datasets.

nature of part of the variability present in the data and allows for the exploration of the experimental heterogeneity. The basic statistical model was as follows:

$$Y = \alpha + \alpha_i + \beta_i \, HCW_i + \gamma_i \, \text{proxy trait}_i + \text{error}.$$

When including an animal typology criterion, it was modified as follows:

$$Y = \alpha + \beta_i \, HCW_i + \gamma_i \, \text{proxy trait}_i + F + \alpha_i(F) + (F \times HCW_i) + (F \times \text{proxy trait}_i) + \text{error}$$

where Y is the response variable, α is the overall intercept, α_i is the effect of study i on the intercept, F is the effect of animal typology criteria, β_i is the coefficient of linear regression of the covariate HCW for the study i, and γ_i is the coefficient of linear regression of the covariate proxy trait for the study i.

For all models, the normality of the residuals was checked. No outliers were identified based on residuals, high leverage, Cook's distance and DEFIT as in Sauvant et al. (2008). To explore the influence of experimental conditions on the residuals, the presence of factors having a significant impact on residuals was tested either by an analysis of variance (for qualitative factors such as animal typology criteria) or by regression (for quantitative factors such as animal performance and carcass characteristics). The quality of fit was evaluated through the adjusted R^2 and the Root Mean Square Error (RMSE).

2.3.4. External validation of the models

The prediction quality of the models presenting the best fit was evaluated using the validation dataset (Supplementary Table S2b and Data S2c). The quality of the predictions was evaluated through several criteria: the coefficient of determination (R^2), the root mean square error (RMSE) and the coefficient of variation of the root mean square error (CV-RMSE), which measure the size of the discrepancies between predicted and observed values, the modeling efficiency (MEF, Loague and Green, 1991), and the mean square prediction error (MSPE) and its components (Bibby and Toutenburg, 1977; Kobayashi and Salam, 2000) as detailed in the Supplementary Data S3. It should be stressed that because of the fixed study effect, the applicability of the models is then limited to the conditions described in the meta-design and cannot be extended to a different population (Sauvant et al., 2008).

3. Results

3.1. Eligible data and range of validity of the models

A preliminary description of all retrieved publications showed a limited amount of data on non-castrated males, regardless of implantation (n = 16 treatments) (for details see Supplementary Tables S2a and S2b). These animals had similar carcass characteristics as those of the implanted castrated males, and their data were grouped together.

The 2 datasets had the same distribution of production purpose and sex of the animals across treatments; however, the distribution of the maturity characteristics of the animals differed slightly (Fig. 2). More importantly, animal performance and most carcass characteristics were similar between datasets despite significantly different ($P < 0.05$) trial lengths, carcass chemical compositions expressed as concentration, and KPH between the datasets (Table 1). These differences may be due to the number of observations which varied from one variable to another in the two datasets (Table 1). Because a few variables were not systematically reported in all publications, the number of available data varied slightly between relationships.

Across both datasets, a very wide range of variation in both live animal and carcass characteristics existed. The average daily gain (ADG) varied between 0.3 and 1.9 kg/d, with the majority of data (81%) ranging between 1 and 1.5 kg/d. The HCW varied between 210 and 431 kg, and the percentage of carcass fat ranged between 15 and 41%. The same trend was found for all other variables correlated with carcass fat weight, such as MAR and SFT, independently of their units. Finally, the majority of data (75%) applied to British breeds or their cross breeds, which showed the greatest carcass fat weight and the lowest HCW and carcass protein weight. The remaining 25% of the data came from Continental breeds and their cross breeds. The absence of multicollinearity between covariates was checked, and HCW was never correlated with YG, SFT and MAR. On the contrary, there was a significant intra-study correlation ($P < 0.000$) between HCW and REA with $R^2 = 0.85$ (Fig. 3).

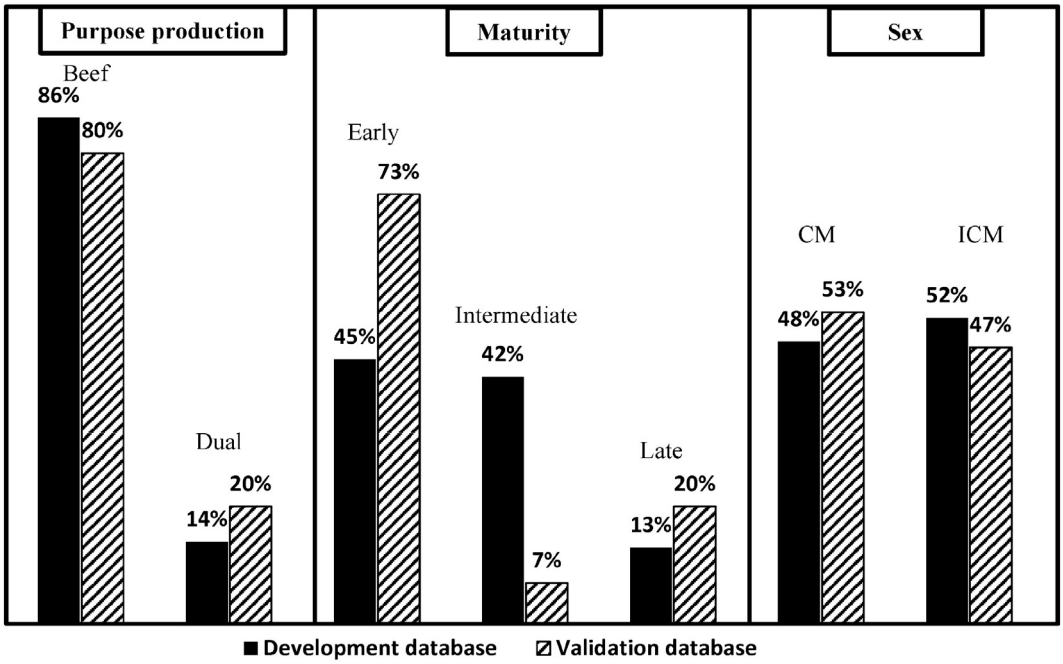


Fig. 2. Description of animal characteristics in the development and validation datasets expressed as proportion of treatments (CM: castrated males and ICM: implanted castrated males).

The relationships between carcass fat weight or carcass protein weight and proxy traits were significant when the classes of publication years (A1, A2 and A3) were introduced into the models. At a similar HCW and EOM, the earlier the publication year, the fatter the animals and the lower their carcass protein weight (results not shown).

3.2. Relationships between carcass fat weight and proxies of carcass fat

All models (Table 2, Supplementary Table S4) showed that each proxy trait was positively related to carcass fat weight except for REA. Generally, REA and even MAR (models 1 to 4 and 5 to 8) were less related to carcass fat weight than SFT or YG (models 9 to 16) based on their high RMSE and the factors influencing the residues. Hence, SFT (models 9 to 12) and YG (models 13 to 16) were the best indicators of carcass fat weight based on their low RMSE (2.83–3.48 vs 4.31–5.72) and their high adjusted R^2 (0.95–0.97 vs 0.86–0.92), with RMSE being more discriminant. The models with SFT and YG had no factors influencing residues except for model 9 (residues were significantly correlated with initial weight and KPH; Supplementary Table S4).

When SFT was used as the main covariate and when studies were nested within an animal typology criterion (models 9 to 12), two of the typology criteria were significant covariates (production purpose and sex), and only one criterion (production purpose) showed a significant interaction with SFT (model 9). The three significant models of SFT (models 9, 10 and 12) had close RMSE values (3.40, 3.47, 3.48), suggesting that SFT is a good predictor for carcass fat regardless of the animal's profile. Model 9 predicted an increase of 27 kg of carcass fat weight per increase of 1 cm SFT at a similar HCW. Model 10 predicted, at a similar HCW, an increase of 27 and 50 kg carcass fat weight for each increment of 1 cm SFT in beef and dual breeds, respectively, or at similar SFT, an increase of 0.29 kg carcass fat weight for each increase of 1 kg HCW regardless of the breed's production purpose.

The models based on YG (models 13 to 16) were even better related to carcass fat weight based on RMSE, as expected from the fact that YG includes the SFT in its construction. Among the criteria of animal typology introduced into the models, production purpose and maturity were significant covariates (models 14 and 15) while sex (model 16) was not, and only one criterion (production purpose) showed a significant interaction with YG. When production purpose was used as a covariate, the model (14) predicted at similar HCW an increase in carcass fat weight of 16 and 26 kg per increase of one unit of YG for beef and dual-purpose breeds, respectively. When maturity was the typology criterion used as a covariate (model 15), an increase of one YG unit at a similar HCW was associated with an increased carcass fat weight of 17 kg regardless of the breed's maturity.

The validation step was only applied to models based on SFT and YG, which presented a reduced RMSE (Fig. 4). The average predicted carcass fat weight was not significantly different from the observed values, the numerical difference being slightly lower with YG than with SFT. All validation criteria (R^2, RMSE, CV-RMSE, MEF, and MSEP) were similar for the models based on YG or SFT with a slight difference in favor of YG because the error due to disturbance (ED) was the main contributor to the MSPE, whereas a slight average error in central tendency (ECT) was detected for the models based on SFT (Supplementary Table S5). Introducing typology criteria into the models did not improve the quality of the predictions (Supplementary Table S5).

3.3. Relationships between carcass protein weight and proxies of carcass protein

In general and whatever the proxy trait considered (Table 3, Supplementary Table S4), the relationships showed a high adjusted R^2 (0.95–0.99). However, and as reported for carcass fat, REA and MAR were less correlated with carcass protein weight than the other proxy traits

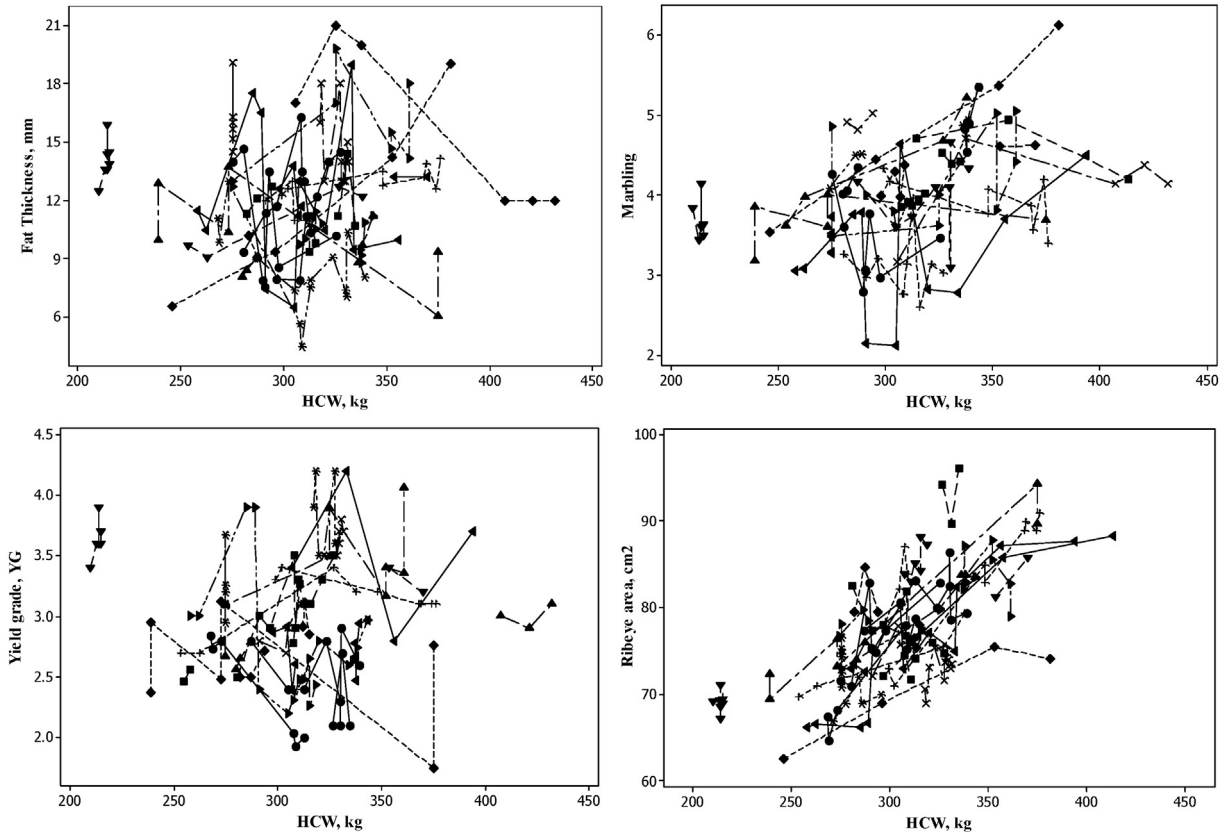


Fig. 3. Meta-design of data according to hot carcass weight (HCW) and the easily obtainable measures; subcutaneous fat thickness, yield grade, marbling or ribeye area in the development dataset.

Table 2
Quantitative relationships between carcass fat weight (kg, as the dependent variable) and hot carcass weight (HCW, kg), a proxy trait [yield grade (YG), subcutaneous fat thickness (SFT), marbling (MAR) or ribeye area (REA)], and an animal typology criteria (refer to Fig. 1 for typology criteria).

N_{model}	Proxy	Typology criteria	Model	Δ value[a]				RMSE	R^2_{adj}
				Groups	Intercept	HCW	Proxy		
1	REA (28, 152)[b]	None	$35.29 \pm 8.67^{***} + 0.56 \pm 0.03^{***}$ HCW $- 1.48 \pm 0.18^{***}$ REA	–	–	–	–	5.74	0.86
2		Purpose	$8.77 \pm 14.12^{NS} + 0.67 \pm 0.06^{***}$ HCW $- 1.60 \pm 0.19^{***}$ REA	Beef	$+36.15 \pm 14.16^{*}$	$-0.10 \pm 0.04^{*}$	NS	5.66	0.86
				Dual	$-36.15 \pm 14.16^{*}$	$+0.10 \pm 0.04^{*}$			
3		Maturity	$-15.19 \pm 11.75^{NS} + 0.59 \pm 0.03^{***}$ HCW $- 0.98 \pm 0.19^{***}$ REA	Early	$+5.92 \pm 1.01^{***}$	NS	NS	4.83	0.90
				Intermediate	$+0.35 \pm 0.65^{NS}$				
				Late	$-6.28 \pm 1.14^{***}$				
4		Sex	$40.35 \pm 7.49^{***} + 0.61 \pm 0.03^{***}$ HCW $- 1.75 \pm 0.16^{***}$ REA	CM	$-22.02 \pm 7.49^{**}$	$+0.17 \pm 0.03^{***}$	$-0.44 \pm 0.16^{**}$	4.92	0.90
				CMI	$+22.02 \pm 7.49^{**}$	$-0.17 \pm 0.03^{***}$	$+0.44 \pm 0.16^{**}$		
5	MAR (25, 125)[b]	None	$-29.60 \pm 6.60^{***} + 0.28 \pm 0.02^{***}$ HCW $+ 9.06 \pm 1.21^{***}$ MAR	–	–	–	–	5.65	0.86
6		Purpose	$-30.46 \pm 6.93^{***} + 0.28 \pm 0.02^{***}$ HCW $+ 9.11 \pm 1.23^{***}$ MAR	Beef	$+2.24 \pm 1.03^{*}$	NS	NS	5.70	0.86
				Dual	$-2.24 \pm 1.03^{*}$				
7		Maturity	$-55.48 \pm 6.80^{***} + 0.40 \pm 0.03^{***}$ HCW $+ 5.89 \pm 1.15^{***}$ MAR	Early	$+7.53 \pm 0.92^{***}$	NS	NS	4.31	0.92
				Intermediate	$-2.24 \pm 0.78^{**}$				
				Late	$-5.33 \pm 1.38^{***}$				
8		Sex	$-30.38 \pm 6.56^{***} + 0.28 \pm 0.02^{***}$ HCW $+ 9.26 \pm 1.21^{***}$ MAR	CM	$+1.19 \pm 0.59^{*}$	NS	NS	5.62	0.86
				CMI	$-1.19 \pm 0.59^{*}$				
9	SFT (26, 146)[b]	None	$-29.34 \pm 4.02^{***} + 0.29 \pm 0.01^{***}$ HCW $+ 2.71 \pm 0.13^{***}$ SFT	–	–	–	–	3.47	0.95
10		Purpose	$-39.14 \pm 5.45^{***} + 0.29 \pm 0.01^{***}$ HCW $+ 3.81 \pm 0.41^{***}$ SFT	Beef	$+11.60 \pm 4.28^{**}$	NS	$-1.16 \pm 0.41^{**}$	3.40	0.95
				Dual	$-11.60 \pm 4.28^{**}$		$+1.16 \pm 0.41^{**}$		
11		Maturity	NS						
12		Sex	$-29.39 \pm 4.03^{***} + 0.29 \pm 0.01^{***}$ HCW $+ 2.71 \pm 0.13^{***}$ SFT	CM	$+0.75 \pm 0.33^{*}$	NS	NS	3.48	0.95
				CMI	$-0.75 \pm 0.33^{*}$				
13	YG (26, 132)[b]	None	$-45.39 \pm 4.80^{***} + 0.29 \pm 0.01^{***}$ HCW $+ 16.26 \pm 0.90^{***}$ YG	–	–	–	–	3.04	0.96
14		Purpose	$-77.82 \pm 11.15^{***} + 0.35 \pm 0.02^{**}$ HCW $+ 20.99 \pm 3.30^{***}$ YG	Beef	$+37.58 \pm 11.15^{**}$	$-0.07 \pm 0.02^{**}$	$-4.96 \pm 2.30^{*}$	2.93	0.96
				Dual	$-37.58 \pm 11.15^{**}$	$+0.07 \pm 0.02^{**}$	$+4.96 \pm 2.30^{*}$		
15		Maturity	$-61.10 \pm 8.31^{***} + 0.33 \pm 0.03^{*}$ HCW $+ 17.32 \pm 1.22^{***}$ YG	Early	$+26.78 \pm 10.55^{**}$	$-0.08 \pm 0.03^{*}$	NS	2.83	0.97
				Intermediate	$+5.59 \pm 9.72^{NS}$	-0.02 ± 0.03^{NS}			
				Late	$-32.37 \pm 15.00^{*}$	$+0.09 \pm 0.04^{*}$			
16		Sex	NS						

NS: not significant: $P > 0.10$, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.
[a] Factor effect on the intercept, the slope of HCW, and the slope of proxy trait.
[b] Number of experimental studies, Number of treatments.

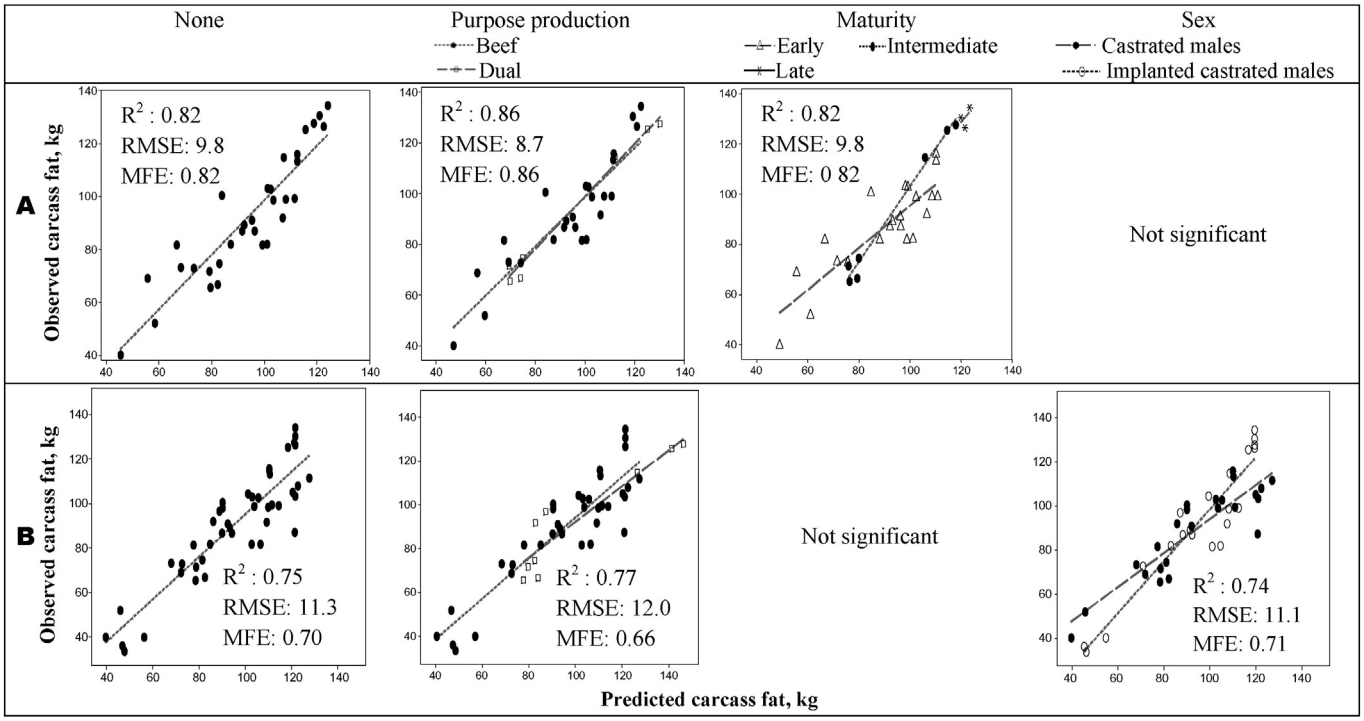


Fig. 4. Relationships between observed vs predicted carcass fat weight, using either yield grade (A) or subcutaneous fat thickness (B) as the proxy traits with or without any animal typology criteria in the models, using the external validation dataset and evaluation by Coefficient de determination (R^2), root mean square error (RMSE), and model efficiency (MEF).

because of higher RMSE. By contrast, YG and SFT (models 25 to 32) presented the lowest RMSE (Table 3). They also showed less interfering factors on the residuals (Supplementary Table S4).

As for carcass fat, YG was best related to carcass protein weight (models 29 to 32) with a low RMSE (Table 3) and no significant factors on the residuals (Supplementary Table S4), followed by SFT (models 25 to 28). Introducing animal typology criteria as a covariate did not modify the quality of fit. Some benefit was noted only when maturity was used as a covariate in the SFT model (27) with the elimination of significant factors on the residuals (Supplementary Table S4). Model 31 predicted that at a similar HCW an increase of one point in YG was associated with a decrease of 4 kg protein whatever the maturity, or that at a similar YG an increase of 1 kg HCW was associated with an increase of 90, 140, and 70 g carcass protein for early, intermediate and late maturity breeds, respectively. Finally, at a similar YG and HCW, the carcass protein weight was predicted to differ significantly across the breed's maturity by 2.4 kg between early and late maturity with the greatest values being for the late maturity breeds.

As previously, the validation steps were applied to Models 25 to 32 (Fig. 5) with SFT and YG as they showed a reduced estimation error. Similarly to carcass fat weight, the mean predicted carcass protein weight was not significantly different from the observed carcass protein weight. The R^2, RMSE, CV-RMSE, MEF, and MSEP for the models with YG or SFT were similar with a slight difference of 13%, 1.4, 0.03, 0.19, and 14.48, respectively, in favor of the models based on YG. The majority of MSPE was associated with the error due to disturbance with a slight proportion of MSPE associated with ECT in the SFT models (Supplementary Table S5). Again, introducing typology criteria into the models did not improve the quality of the predictions (Supplementary Table S5).

4. Discussion

This meta-analysis combined results from 41 independent studies to establish and validate the quantitative relationships between the chemical composition of carcasses and proxy traits in growing-finishing male cattle accounting for the effect of animal typology. The relatively small number and old publication years of eligible publications were mainly because reference measures of the chemical composition of the carcass are not used often anymore because of cost and workload. All publications originated from the U.S.A. where studies generally measure the chemical composition of the whole carcass, whereas studies from European countries for example more often measure the physical tissue composition of the carcass. The eligible publications used a majority of British breeds and their crosses (75% of data) and a minority of Continental breeds (25% of data). The lack of balanced data between Continental and British breeds is one of the limitations of the present work as well as the dearth of data on females. Hence, the models obtained apply to male animals with light and fatty carcasses (Adams, Garrett, and Elings, 1973). They also apply to animals presenting growth rates (averaging 1238 g/d, with 90% of data above 1000 g/d) compatible with real-world practices.

Generally, significant relationships were obtained between proxy traits and carcass fat and carcass protein weight. The relevance of each covariate is discussed further below. Most proxy traits (YG, SFT, MAR but not REA) were positively related to carcass fat weight and negatively related to carcass protein weight, consistent with the negative correlations that exist between the proportions of adipose tissue and muscle at similar carcass weights (Robelin, 1986a).

4.1. Hot carcass weight: significant covariate

HCW proved to be a significant covariate in all models as expected from its important relationship with the growth of the different carcass compartments. It was even more related to carcass protein weight than to carcass fat weight, as also noted by Al-Jammas, Agabriel, Vernet, and Ortigues-Marty (2015) in similar relationships applied to the tissue composition of the carcass. Indeed, when considering the weight of tissues, both muscle and fat tissue weights increased with HCW, explaining why HCW was positively related to both the carcass fat and carcass protein weights in all models. In normal slaughter

Table 3
Quantitative relationships between carcass protein weight (kg, as the dependent variable) and hot carcass weight (HCW, kg), a proxy trait [yield grade (YG), subcutaneous fat thickness (SFT), marbling (MAR) or ribeye area (REA)], and an animal typology criteria (refer to Fig. 1 for typology criteria).

N_{model}	Proxy	Typology criteria	Model	Δ value[a]				RMSE	R^2_{adj}
				Groups	Intercept	HCW	Proxy		
17	REA (19, 97)[b]	None	$-6.27 \pm 2.54^{***} + 0.04 \pm 0.01^{***}$ HCW $+ 0.48 \pm 0.06^{***}$ REA	–	–	–	–	1.37	0.95
18		Purpose	$-5.80 \pm 2.69^{*} + 0.04 \pm 0.01^{***}$ HCW $+ 0.48 \pm 0.06^{***}$ REA	Beef	$-0.47 \pm 0.21^{*}$	NS	NS	1.39	0.95
				Dual	$+0.47 \pm 0.21^{*}$				
19		Maturity	$-0.60 \pm 17.45^{NS} + 0.09 \pm 0.05^{¤}$ HCW $+ 0.24 \pm 0.07^{**}$ REA	Early	$+15.80 \pm 17.08^{NS}$	-0.05 ± 0.05^{NS}	NS	1.13	0.97
				Intermediate	$+3.47 \pm 16.90^{NS}$	-0.01 ± 0.05^{NS}			
				Late	-19.27 ± 33.80^{NS}	$+0.07 \pm 0.10^{NS}$			
20		Sex	$-12.20 \pm 2.88^{***} + 0.05 \pm 0.01^{***}$ HCW $+ 0.52 \pm 0.06^{***}$ REA	CM	$+8.93 \pm 2.34^{***}$	$-0.03 \pm 0.01^{***}$	NS	1.28	0.96
				CMI	$-8.93 \pm 2.34^{***}$	$+0.03 \pm 0.01^{***}$			
21	MAR (16, 79)[b]	None	$12.83 \pm 1.79^{***} + 0.15 \pm 0.01^{***}$ HCW $- 3.40 \pm 0.31^{***}$ MAR	–	–	–	–	1.23	0.97
22		Purpose	NS						
23		Maturity	$14.64 \pm 2.17^{***} + 0.13 \pm 0.01^{***}$ HCW $- 2.73 \pm 0.44^{***}$ MAR	Early	$-1.67 \pm 0.36^{***}$	NS	NS	1.14	0.98
				Intermediate	$+2.41 \pm 0.28^{***}$				
				Late	-0.74 ± 0.55^{NS}				
24		Sex	$13.16 \pm 1.76^{***} + 0.15 \pm 0.00^{***}$ HCW $- 3.47 \pm 0.30^{***}$ MAR	CM	$-0.82 \pm 0.17^{***}$	NS	NS	1.20	0.97
				CMI	$+0.82 \pm 0.17^{***}$				
25	SFT (18, 94)[b]	None	$11.85 \pm 1.51^{***} + 0.14 \pm 0.01^{***}$ HCW $- 0.73 \pm 0.05^{***}$ SFT	–	–	–	–	0.85	0.98
26		Purpose	$7.58 \pm 2.17^{**} + 0.15 \pm 0.01^{***}$ HCW $- 0.74 \pm 0.04^{***}$ SFT	Beef	$+6.76 \pm 2.16^{**}$	$-0.02 \pm 0.00^{**}$	NS	0.85	0.98
				Dual	$-6.76 \pm 2.16^{**}$	$+0.02 \pm 0.00^{**}$			
27		Maturity	$8.18 \pm 13.30^{NS} + 0.14 \pm 0.04^{***}$ HCW $- 0.57 \pm 0.13^{***}$ SFT	Early	$+19.97 \pm 13.42^{NS}$	-0.07 ± 0.04^{NS}	$+0.10 \pm 0.13^{NS}$	0.69	0.99
				Intermediate	$+3.24 \pm 13.34^{NS}$	$+0.00 \pm 0.04^{NS}$	$-0.35 \pm 0.14^{*}$		
				Late	-23.22 ± 26.51^{NS}	$+0.07 \pm 0.08^{NS}$	$+0.26 \pm 0.25^{NS}$		
28		Sex	$9.37 \pm 2.08^{***} + 0.14 \pm 0.01^{***}$ HCW $- 0.73 \pm 0.04^{***}$ SFT	CM	$+3.21 \pm 2.04^{¤}$	$-0.01 \pm 0.01^{¤}$	NS	0.89	0.98
				CMI	$-3.21 \pm 2.04^{¤}$	$+0.01 \pm 0.01^{¤}$			
29	YG (18, 84)[b]	None	$15.56 \pm 1.54^{***} + 0.14 \pm 0.00^{***}$ HCW $- 4.41 \pm 0.25^{***}$ YG	–	–	–	–	0.66	0.99
30		Purpose	NS						
31		Maturity	$28.19 \pm 18.54^{NS} + 0.10 \pm 0.05^{*}$ HCW $- 3.99 \pm 0.45^{***}$ YG	Early	$+2.93 \pm 18.9^{NS}$	-0.01 ± 0.06^{NS}	NS	0.65	0.99
				Intermediate	-14.27 ± 18.57^{NS}	$+0.04 \pm 0.05^{NS}$			
				Late	$+11.34 \pm 36.93^{NS}$	-0.03 ± 0.10^{NS}			
32		Gender	$15.50 \pm 1.55^{***} + 0.14 \pm 0.00^{***}$ HCW $- 4.42 \pm 0.25^{***}$ YG	CM	$+0.36 \pm 0.10^{**}$	NS	NS	0.66	0.99
				ICM	$-0.36 \pm 0.10^{**}$				

NS: not significant: $P > 0.10$, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.
[a] Factor effect on the intercept, the slope of HCW, and the slope of proxy trait.
[b] Number of experimental studies, Number of treatments.

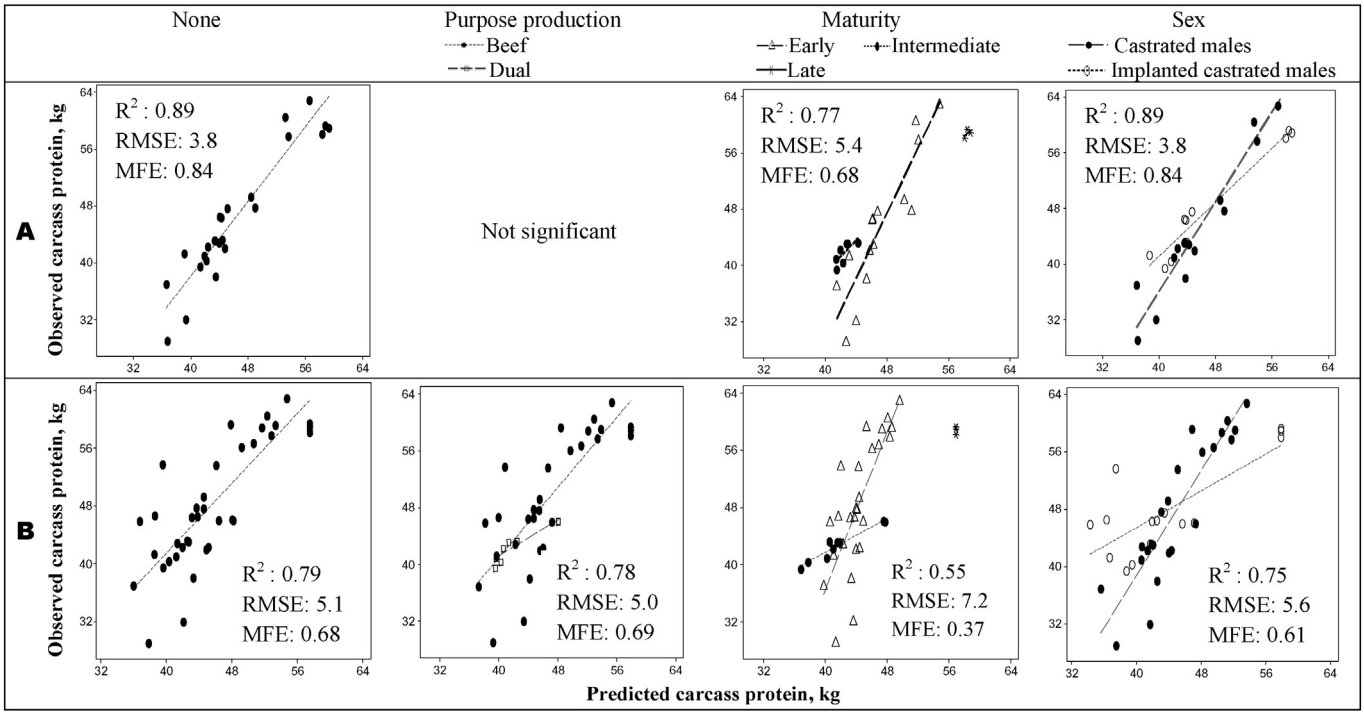


Fig. 5. Relationships between observed vs predicted carcass protein weight, using either yield grade (A) or subcutaneous fat thickness (B) as the proxy traits with or without any animal typology criteria in the models, using the external validation dataset and evaluation by Coefficient de determination (R^2), root mean square error (RMSE), and model efficiency (MEF).

ranges (350–700 kg depending on the production system), the allometric coefficients were greater than 1.0 for the fat depots but lower than 1.0 for bone and muscle, indicating that the latter grow more slowly than the carcass (Keane and Allen, 2002). In other words, as carcass weight increases, the percentage of muscle decreases while the percentage of fat increases (Arboitte et al., 2004; Charles and Johnson, 1976; Warriss, 2010). The significance of HCW as a covariate varied slightly with the animal typology criteria considered in the relationships.

4.2. Animal typology criteria did not significantly improve the quality of models

The first challenge of the present study was to aggregate and analyze published data from a wide variety of animals in a rigorous manner using objective and synthetic criteria. We propose here an animal typology that allows breeds or crosses to be described based on four criteria (out of all characteristics gathered) instead of simply using their names. Due to the lack of animal description in the publications and of quantitative criteria to evaluate the speed of maturity for instance, empirical expertise of the authors had to be used.

Application of the typology to the dataset was easier with purebreds (58% of data) because their characteristics are better known. In its application to cross-breeds (42% of data) we assumed that the genetic crossing aimed to combine the best characteristics of each breed. For instance, the cross-breeds between British breeds, which are small and early maturity, and Continental breeds, which are larger, and late maturity were assumed to show a medium-size frame and intermediate maturity (Supplementary Data S1).

A preliminary analysis of the development dataset had indicated that the relationships between the proxy traits and carcass chemical composition were significantly ($P < 0.001$) affected by breed and animal characteristics, and we had assumed that the inclusion of these characteristics as covariates in the models would significantly improve the prediction quality of the models. No significant improvement was noted, probably because some confounding factors remain due to the lack of balanced data between the different typology criteria.

The genetic improvement of animals (Felius, Koolmees, Theunissen, Consortium, and Lenstra, 2011) could only be approached by analyzing the year of publication. The classes of publication years were significant covariates when included in the models. This effect was strictly associated with the significant increase in carcass weight at each decade because the percentage of carcass fat did not change over the years in our dataset. Anderson, Hawkins, Bergen, and Merkel (1988) had also noted that the pattern of fat deposition and the relationship among the fat depots had not changed since 1946. In addition to the imbalance in the dataset mentioned earlier, some methodological biases could not be excluded with the evolution of the reference methods to evaluate carcass composition. As a result, this effect was not further explored.

4.3. Least satisfactory relevance of REA and MAR to predict carcass chemical composition

REA and MAR, in combination with HCW, were the least satisfactory predictors for the carcass fat and carcass protein weights as shown by their highest RMSE. These results obtained across studies confirm the within-study results obtained by Cole, Ramsey, and Epley (1962) and Kent, Davis, Ramsey, and Schluter (1991) in single breeds and with animals similarly managed. The residuals from the present models were significantly influenced by factors which reflect fat depots in other anatomical sites (YG, KPH, and SFT). Therefore, MAR or REA, in combination with HCW, are not sufficient to predict changes in either carcass fat weight or in carcass protein weight (Johnson and Baker, 1997). Generally, the use of REA or MAR in multiple regressions with other carcass measurements led to modest improvements in the accuracy of prediction (O'Mara et al., 1998) with R^2 increasing from 0.76 to 0.78.

REA supposedly provides an indication of the muscling status of the carcass (Johnson and Baker, 1997), but in our results REA was a poor predictor of the carcass composition, probably due to the correlation

between REA and HCW (Fig. 2). This proxy trait may also be biased by the rib number (Hopkins and Roberts, 1995). Out of the 28 studies eligible for the REA models, one used the 8th rib and 3 did not define the rib number. They may also be biased by animal characteristics and management practices. In small-frame cattle as in our dataset (75% of the data) the ribeye area tends to grow at a slower rate than in large-frame cattle, while fat depot is faster in small-frame than in large-frame cattle (Johnson, Taylor, Priyanto, and Meehan, 1992). In addition, in the small-frame cattle, REA does not vary in the finishing stages to the contrary of fat deposition (Huffman, 1991).

Marbling, an indicator developed in relation to meat quality (Indurain et al., 2009), describes the amount and distribution of visible intramuscular fat tissues (Dow, Wiegand, Ellersieck, and Lorenzen, 2011). These adipose tissues contribute the least to total carcass fat compared with other fat tissues and grow last after the internal, intermuscular and subcutaneous fat tissues (Robelin, 1986b). Marbling may also be biased by the rib number (Zembayashi, Nishimura, Lunt, and Smith, 1995). Marbling was found to be a significant predictor of carcass fat tissues or muscle percentage when combined with both KPH and YG in the models of prediction, but it did not greatly improve the quality of prediction (O'Mara et al., 1998).

4.4. Subcutaneous fat thickness as a predictor of carcass chemical composition

The prediction of carcass fat weight from SFT had a lower RMSE than from MAR and REA in agreement with several results (Cole et al., 1962; Indurain et al., 2009; May et al., 2000). The quantity of subcutaneous adipose tissue is positively related to total adipose tissue depots between birth and adult age (Robelin and Casteilla, 1990). The R^2 of such relationships varies between breeds, from 0.78 for Charolais to 0.90 for Angus and Hereford (Charles and Johnson, 1976). This explains why in all SFT models, this covariate combined with HCW accounted for the majority of the changes in carcass fat weight as also reported by Houghton, Lemenager, Moss, and Hendrix (1990). The subcutaneous fat tissue represents on average between 10 to 12% of total carcass fat tissues. It is a late-developing fat tissue. It is also one of the fat tissues, along with the internal fat tissues, that is most affected by environmental factors and breed effects, mostly during the fattening period (Charles and Johnson, 1976). Similarly, SFT is a good predictor of carcass protein weight, confirming the results by Crouse et al. (1974) and Powell and Huffman (1973).

Adding a typology criterion as a covariate improved the biological significance of the models but did not significantly improve the quality of prediction as discussed above. The production purpose was a significant covariate when introduced in the SFT model, indicating significant differences between dual-purpose breeds and beef breeds. The parameter values obtained for dual-purpose breeds were closer to those for purebred dairy breeds than for beef breeds. Indeed, in our dataset, 98% of the dual-purpose breeds were crosses between beef and dairy breeds, and Kempster (1981) had demonstrated that the dairy × beef crosses (Friesian × Angus or × Charolais) had similar fat distribution to dairy (Friesian) purebreds. Generally, dairy cattle tend to deposit a lower proportion of total fat as subcutaneous and intermuscular fat and more as internal fat as KPH (Kempster, Cuthbertson, and Harrington, 1976). This explains why the slope and intercept of the SFT models were influenced by the breed's production purpose (Model 13). Generally, the intercept value for dual-purpose breeds (−50.74) was lower than for beef breeds (−27.54) (Model 13), indicating a greater carcass fat weight for beef compared with dairy (cross) breeds at similar SFT. The absence of an HCW × production purpose interaction implies that the differences in carcass fat weight were constant throughout the range of fat thickness values. These results converge with those of Charles and Johnson (1976).

The implant status had a significant effect in the SFT models. The absolute amount of carcass fat was significantly different between CM and ICM as indicated by the variation in intercept. Our results showed that in steers the implant treatment decreased the weight of carcass fat by 3% at a similar SFT and HCW. These results corroborate those of Bruns et al. (2005).

4.5. Yield grade as a predictor of carcass chemical composition

Finally, and among all EOM tested, YG was the best predictor of carcass fat and carcass protein weights. It was created to estimate the percentage of the four carcass pieces, which are the most representative of the commercial carcass value, the closely trimmed boneless round, loin, rib, and chuck (USDA, 1965). By construction, YG includes all previous measures except for marbling, namely HCW, SFT and REA, while adding KPH in its formula. Hence, it is calculated from indicators that reflect carcass tissue mass, the subcutaneous and the internal adipose tissues as well as the muscling of the carcass. Only the intermuscular adipose tissue was not included in the YG formula despite representing up to 70% of total adipose tissue weight. This adipose tissue, however, is known to be highly related to HCW and affected little by other factors of variation (Robelin, 1986b). It is noteworthy that although HCW is included in the calculation of YG, both variables were independent, and the inclusion of HCW as a covariate in our models was significant ($P < 0.05$). The conclusion that YG was the best predictor applies to different breeds (British, Continental or British × Continental crossbreeds); however, it would need to be further tested in Continental breeds and under different husbandry and slaughter conditions. As reported by Abraham, Carpenter, King, and Butler (1968), the YG defined by the USDA was more acceptable for British breeds (such as Angus and Herefords) and British × Continental crossbreeds than for Continental breeds (such as Charolais).

5. Conclusions

The present results show that the chemical composition of the carcass can be predicted from proxy traits and that the quality of prediction is better from YG and SFT with prediction errors averaging 11 and 12% of carcass fat and 9 and 12% of carcass protein, respectively. The choice of proxy for predicting the chemical composition of the carcass depends on the objective and on the animals. If the objective is to review and analyze published data by meta-analysis, published results on YG and SFT can be used and combined with published direct measures of carcass protein and carcass fat. These results apply to animals having the same characteristics as those used in the present study, mainly characterized by rather light and fatty carcasses from early-maturing British breeds. If the objective is to evaluate carcass composition in live animals under experimental or farm conditions, either one of the two proxy traits, YG and SFT, can be used to predict the carcass composition for groups of animals. The choice of proxy will depend on the stage of growth, which determines the site of major fat depots. Subcutaneous fat can be used as a predictor only at the finishing stages when the subcutaneous fat depots are predominant. Finally, the proxy traits which were developed as indicators of meat quality, MAR and REA, were poorer predictors of carcass fat and protein weights. The introduction of typology criteria into the models did not improve the prediction quality, probably because of the limited and imbalanced database. This work would need to be extended to animals from late-maturing breeds and dairy breeds presenting heavy carcass weight but low carcass fat. However, considering the available data, it could only apply to the physical tissue composition of the carcass instead of its chemical composition. Indeed, all research with late-maturing breeds measured physical tissue composition rather than the chemical composition of the carcass.

Conflict of interest

The authors state that they have no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.meatsci.2016.04.029.

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