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Breeding for beef quality traits using NIRS

**The relevance of near-infrared reflectance spectroscopy predictions as indicator traits in
breeding programs for enhanced beef quality¹**

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ABSTRACT: The aims of this study were 1) to investigate the potential application of near-infrared spectroscopy (NIRS) to predict beef quality (BQ) traits, 2) to assess genetic variations of BQ measures and their predictions obtained by NIRS, and 3) to infer the genetic relationship between measures of BQ and their predictions. Young Piemontese bulls (N = 1,230) were raised and fattened on 124 farms, and slaughtered at the same commercial abattoir. Beef quality traits were shear force (SF, kg), cooking loss (CL, %), drip loss (DL, %), lightness (L*), redness (a*), yellowness (b*), saturation index (SI), and hue angle (H). Near-infrared spectra were collected using a Foss NIRSystems 5000 over a spectral range of 1,100 to 2,498 nm every 2 nm, in reflectance mode. After editing, prediction models were developed on a calibration subset (N = 268) using partial least squares (PLS) regressions, followed by application of these models to the validation subset (N = 940). Estimation of (co)variance for measures of BQ and NIRS-based predictions was obtained through a set of bivariate Bayesian analyses on the validation subset. Near-infrared predictions were satisfactory for measurements of L* ($R^2 = 0.64$), a* ($R^2 = 0.68$), H ($R^2 = 0.81$), and SI ($R^2 = 0.59$), but not for b*, DL, CL, and SF. The loss of additive genetic variance of predicted versus measured L*, a*, DL, CL, and SF was generally high and similar to the loss of residual variance, being a function of the calibration parameter R^2 . As a consequence, estimated heritabilities of measures and predictions of BQ were similar for traits with high calibration R^2 values. Genetic correlations between BQ measures and predictions were high for all color traits and DL, and higher than the corresponding phenotypic correlations, whereas both the phenotypic and genetic correlations for SF and CL were nil. Results suggest that NIRS-based predictions for color features and DL may be used as indicators traits to improve meat quality of Piemontese breed.

Key words: genetic parameter, meat quality, near-infrared spectroscopy, Piedmontese

INTRODUCTION

Beef quality (BQ) traits are important aspects of beef production from the consumer viewpoint and with respect to related effects on herd profitability (Dikeman, 1990). As exploitable additive genetic variation for BQ exists (Burrow et al., 2001; Johnston et al., 2003; Warner et al., 2010), it is expected that such traits may be enhanced through selection strategies. However, large-scale recording of individual BQ phenotypes remains a critical issue because the available techniques are time-consuming and, as yet, no high-throughput automated measuring device has been developed. As opportunities for breeding based on direct measures of BQ phenotypes are limited, optimal selection to enhance BQ remains under investigation.

Alternative methodologies for measuring BQ rely on the use of infrared spectroscopy (Prevolnik et al., 2004; Prieto et al., 2009). Because the technique is rapid and accurate, infrared spectroscopy has been successfully used in the beef industry for chemical analysis (Mitsumoto et al., 1991; Osborne et al., 1993; Hildrum et al., 1995). Conversely, near-infrared spectroscopy (NIRS) is less reliable in predicting technological parameters of meat and meat products (Albeni and Bergoglio, 2001; Geesink et al., 2003; Hoving-Bolink et al., 2005).

From a genetic point of view, the relevance of NIRS in programs focusing on selection for improved BQ relies on genetic variation of NIRS-based predictions of BQ and on the magnitude of genetic correlation between NIRS-based predictions and BQ measured by defined reference methods. No estimates of such genetic parameters are currently available for BQ. We therefore investigated the ability of NIRS to predict BQ, the genetic variations in BQ measures and their

predictions obtained by NIRS and the genetic relationship between measures of BQ and predictions.

MATERIALS AND METHODS

Animals, samples, and data

The present study was part of a wider project conducted on 1,230 young Piedmontese bulls marketed as “Vitellone Piemontese della Coscia” under a Protected Geographical Indication (PGI), as defined by the European Union. Animals were fattened on 124 farms and slaughtered at the same commercial abattoir from March 2005 to February 2007. The average age at slaughter (SD) was 523 d (73 d). Young bulls were progeny of 109 AI purebred sires and 1,170 dams, all registered in the Italian Piedmontese herdbook. Sire-offspring relationships were ascertained using DNA testing based on 19 microsatellites (Budowle et al., 2005).

Twenty-four hours after slaughter, individual samples (one per animal) of the Longissimus thoracis muscle were collected between the fifth and sixth thoracic vertebrae, weighed, individually vacuum-packed, and transferred to the meat laboratory of the Department of Animal Science of the University of Padova (Legnaro, Italy) using a portable cooler (4°C). Upon arrival, samples were stored at 4°C in a chilling room until measurement of BQ traits.

Physical analysis and near-infrared spectroscopy

After aging for 8 d, BQ of meat samples was assessed by measurement of color, drip loss (DL, %), cooking loss (CL, %), and shear force (SF, kg). Drip loss was computed as the difference between the weight of the packaged sample and the weight of the sample dried using blotting-paper plus the weight of the heat-dried bag, and expressed as a percentage of sample

weight. Two slices of meat, each 20-mm thick, were cut from each sample. The first slice was exposed to air at 4°C for 1 h (ASPA, 1996), and the color of the exposed surface was determined using a Minolta CM-508 spectrophotometer (Konica Minolta, Milan, Italy), equipped with a D65 light source. The reflectance coordinates (L^* , a^* , b^*) of the Commission Internationale de l'Éclairage (CIE, 1976) were measured at five random positions. Saturation index (SI) was calculated using the formula $SI = \sqrt{a^{*2} + b^{*2}}$, whereas hue angle (H) was calculated from the formula $H = \tan^{-1}(b^*/a^*)$ (AMSA, 1991). The parameters L^* , a^* , b^* , SI, and H were measured five times each and the measures were averaged prior to statistical analysis. The second slice was weighed, sealed in a polyethylene bag, heated in a water bath at 75°C for 55 min, and weighed again for measurement of cooking loss (ASPA, 1996). Cooking loss was computed as the amount of weight lost after cooking as a percentage of the weight of the uncooked slice. Shear force was measured on five 1-cm² cross-sectional round cores, taken at approximately the same location from each cooked slice and running parallel to the longitudinal axis of the muscle fibers, using a TA-HDi Texture Analyzer (Stable Micro System Ltd., Godalming, UK), equipped with a Warner-Bratzler shear device (100 kg load cell and crosshead speed of 2 mm/sec). Both CL and SF were measured five times each and measures were averaged prior to statistical analysis.

Near-infrared spectra were collected on fresh minced samples using a Foss NIRSystems 5000 over a spectral range of 1,100 to 2,498 nm, in reflectance mode, every 2 nm. Duplicate spectra were captured for each sample and averaged prior to data analysis.

Statistical analysis

Validation procedure. The original dataset was edited to discard records with errors (*e.g.*, individual identification spectra not matching reference samples). After editing, a total of 1,208

records, including measures of BQ and NIRS spectra, were available for statistical analysis. To evaluate the predictive ability of NIRS measurements for BQ traits and the magnitude of genetic correlations between BQ measurements and predictions from calibration equations based on NIRS spectra, a holdout validation procedure was carried out. This method involved the partition of data into two subsets, a calibration and a test subset. The former was used to develop a calibration equation that could predict individual BQ phenotypes using NIRS spectra, whereas the latter was employed to validate the calibration equation and to estimate heritabilities and genetic correlations for measured BQ traits and predictions obtained from NIRS spectra and the calibration equations. Observations to be included in the calibration subset were randomly sampled from the set of available data with the restriction that at least 2 observations per herd and week of laboratory analysis were present in the subset (268 records). Records not included in the calibration subset were included in the test subset (940 records).

Multivariate data analysis and predictive ability of NIRS. Partial least squares (PLS) regressions (Unscrambler software, v.9.6; Camo A/S, Oslo, Norway) were used to establish calibration models (Hubert and Van den Branden, 2003). Partial least squares regressions have been used to estimate correlations between reference data and values predicted from spectral information in meat (Prieto et al., 2008) and milk (Soyeurt et al., 2006).

Models were developed using untreated spectral data (absorbance spectra) for CL, DL, and color traits, and untreated spectral data plus first derivative spectra for SF. To assess the adequacy of the calibration models, we calculated the root mean square error of calibration (RMSEC) and the coefficient of determination (R^2). To evaluate the practical utility of the models, the range error ratio (RER) was calculated as the ratio between the range and the RMSEC of the trait (Williams, 1987). Models with RER values lower than 3 have little practical utility; RER values between 3

and 10 indicate limited to good practical utility; and RER values above 10 indicates high utility value of the model (Williams, 1987).

Estimates of (co)variance components. For test subset (N = 940 records), (co)variance components and related parameters were estimated using a Bayesian approach and Markov-chain Monte Carlo (MCMC) methods (Sorensen and Gianola, 2002). A Bayesian technique was used because this offers some advantages over classical statistical methods (Blasco, 2005); in particular, Bayesian inference is based on probabilities, providing great flexibility in the construction of all types of confidence intervals. (Co)variance components for measures of BQ and predictions by NIRS were estimated using eight separate bivariate Bayesian analyses on the test subset. For all traits, the model included the effects of fattening farms (124 levels), week of BQ laboratory analysis (92 weeks), and carcass weight (class 1: < 387 kg; class 2: 387 to 410 kg; class 3: 411 to 430 kg; class 4: 431 to 450 kg; class 5: 451 to 474 kg; class 6: > 474 kg). All traits were continuous variables and the values were assumed to be sampled from the following normal multivariate distribution:

$$p\left(\begin{bmatrix} \mathbf{y}_{\text{BQ}} \\ \mathbf{y}_{\text{pBQ}} \end{bmatrix} \mid \mathbf{b}, \mathbf{c}, \mathbf{q}, \mathbf{u}, \mathbf{R}\right) \sim \text{MVN}\left(\begin{bmatrix} \mathbf{X}\mathbf{b}_{\text{BQ}} + \mathbf{W}_{11}\mathbf{c}_{\text{BQ}} + \mathbf{W}_{21}\mathbf{q}_{\text{BQ}} + \mathbf{Z}_1\mathbf{u}_{\text{BQ}} \\ \mathbf{X}\mathbf{b}_{\text{pBQ}} + \mathbf{W}_{12}\mathbf{c}_{\text{pBQ}} + \mathbf{W}_{22}\mathbf{q}_{\text{pBQ}} + \mathbf{Z}_2\mathbf{u}_{\text{pBQ}} \end{bmatrix}, \mathbf{I} \otimes \mathbf{R}\right),$$

where \mathbf{y}_{BQ} is a vector of phenotypic observations on measures of BQ; \mathbf{y}_{pBQ} is a vector of phenotypic observations on NIRS-based predictions of BQ; \mathbf{X} , \mathbf{W}_1 , \mathbf{W}_2 , and \mathbf{Z} are incidence matrices relating systematic ($\mathbf{b}' = [\mathbf{b}'_{\text{BQ}} \mathbf{b}'_{\text{pBQ}}]$), fattening herd ($\mathbf{c}' = [\mathbf{c}'_{\text{BQ}} \mathbf{c}'_{\text{pBQ}}]$), week of laboratory analysis ($\mathbf{q}' = [\mathbf{q}'_{\text{BQ}} \mathbf{q}'_{\text{pBQ}}]$), and additive genetic ($\mathbf{u}' = [\mathbf{u}'_{\text{BQ}} \mathbf{u}'_{\text{pBQ}}]$) effects to the vector of

observations; \mathbf{I} is an identity matrix of appropriate order; and \mathbf{R} is a 2 x 2 matrix of residual (co)variances. The systematic effect considered in \mathbf{b} is the carcass weight.

Flat priors were used for systematic effect and dispersion parameters. Prior distributions for the additive genetic effects in \mathbf{u} , herd effects in \mathbf{c} , and weeks of laboratory analysis in \mathbf{q} , were normal densities. In a Bayesian setting, we assumed:

$$p(\mathbf{u} | \mathbf{A}, \mathbf{G}) \sim N(0, \mathbf{A} \otimes \mathbf{G}),$$

where \mathbf{G} is a 2 x 2 additive genetic (co)variance matrix, and \mathbf{A} the numerator relationship matrix between individuals. Likewise, herd effects and week of laboratory analysis were assumed to follow normal bivariate distributions:

$$p(\mathbf{c} | \mathbf{I}, \mathbf{P}_1) \sim N(0, \mathbf{I} \otimes \mathbf{P}_1),$$

$$p(\mathbf{q} | \mathbf{I}, \mathbf{P}_2) \sim N(0, \mathbf{I} \otimes \mathbf{P}_2),$$

where \mathbf{P}_1 is a 2 x 2 herd (co)variance matrix and \mathbf{P}_2 is a 2 x 2 week of the laboratory analysis (co)variance matrix.

Gibbs sampler. Marginal posterior distributions of unknown parameters were estimated by performing numerical integration using the Gibbs sampler (Gelfand and Smith, 1990), as implemented in the TM program (<http://snp.toulouse.inra.fr/~alegarra/>). This was employed to obtain auto-correlated samples from the joint posterior distributions and subsequently from the marginal posterior distributions of all unknowns in the model. The lengths of the chain and of the burn-in period were assessed by visual inspection of trace plots, as well as by the diagnostic tests of Geweke (1992) and Gelman and Rubin (1992). After a preliminary run, we decided to construct a single chain consisting of 850,000 iterations and to discard the first 50,000 iterations as a very conservative burn-in. Subsequently, one of every 200 successive samples was retained, to store draws that were more loosely correlated. Thus, 4,000 samples were used to determine

posterior distributions of unknown parameters. The lower and upper bounds of highest 95% probability density regions for h^2 and additive genetic and residual variances were obtained from the estimated marginal densities as well as from a posterior probability for $h^2 > 0.10$. The posterior median was used as the point for estimating (co)variance components and related parameters. Auto-correlations between samples and estimates of Monte Carlo Standard Error (Geyer, 1992) were calculated.

To facilitate comparisons with previously reported results, we calculated intraherd heritability as:

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2}$$

where σ_a^2 is the additive genetic variance and σ_e^2 is the residual variance. Genetic correlations were computed as:

$$r_a = \frac{\sigma_{a1,a2}}{\sigma_{a1} \cdot \sigma_{a2}}$$

where $\sigma_{a1,a2}$ is the additive genetic covariance between traits 1 and 2, and σ_{a1} and σ_{a2} are the additive genetic standard deviations of traits 1 and 2, respectively. Phenotypic correlations were computed as:

$$r_p = \frac{\sigma_{p1,p2}}{\sigma_{p1} \cdot \sigma_{p2}}$$

where $\sigma_{p1,p2}$ is the phenotypic covariance between traits 1 and 2, and σ_{p1} and σ_{p2} are the phenotypic standard deviations of traits 1 and 2, respectively.

RESULTS AND DISCUSSION

The Piedmontese (Piemontese) is the most important Italian beef cattle breed, characterized by muscular hypertrophy (Kambadur et al., 1997), and is actively selected for traits such as daily weight gain, live fleshiness (Albera et al., 2001; Mantovani et al., 2010), and direct and maternal calving performance (Carnier et al., 2000; Kizilkaya et al., 2002; 2003). Previous investigations have assessed phenotypic variation in carcasses (Biagini and Lazzaroni, 2005; Dal Maso et al., 2009; Schiavon et al., 2010a) and BQ traits (Destefanis et al., 2003; Schiavon et al., 2010b) of purebred Piedmontese cattle. Conversely, genetic aspects of BQ traits have been studied only in crossbreeding experiments (Wheeler et al., 2001b), thus not at a population level.

To address this issue, a research project has been established in cooperation with the National Association of Piedmontese Breeders (ANABoRaPi, Carrù, Italy), to study the genetics of BQ traits in this breed, both quantitatively (Boukha et al., 2007) and at a molecular level (Ribeca et al., 2009). The possibility of estimating BQ traits using NIRS forms the topic of the present report. The data obtained from BQ analyses (Table 1) were similar to those obtained on other hypertrophic breeds (Vincenti et al., 2007), especially Belgian Blue cattle (Fiems et al., 2003).

Predictions of beef quality traits

Descriptive statistics for the calibration and test subsets are presented in Table 1. The means and coefficients of variation (CVs) of BQ traits in the two subsets were similar. The CVs were quite high and ranged from 9.26 (H) to 33.23% (DL), facilitating the development of robust calibration equations.

The coefficients of determination of calibration (R^2) varied from 0.44 to 0.81 for color indices, but were very low ($R^2 < 0.25$) for DL, CL, and SF (Table 1). The RMSECs varied from

1.41 to 2.12 for color indexes and were 1.19%, 3.55%, and 0.48 kg for DL, CL, and SF, respectively. The range error ratio (RER) values varied from 5.15 (CL) to 12.18 (H), showing limited-to-good practical utility of the prediction models. Except for b^* , the R^2 values of all color indices were quite high (0.59 to 0.81), indicating that NIRS could predict these traits satisfactorily (Williams, 2003). NIRS-based predictions were much less accurate for DL, CL, and SF ($R^2 < 0.25$). In general, predictions from the present work were less accurate than those reported by Leroy et al. (2003), Andrés et al. (2008), and Prieto et al. (2008, 2009), but more accurate than values of Hoving-Bolink et al. (2005). The low accuracy of NIRS-based predictions for DL and CL is in agreement with data reported previously (Leroy et al., 2003; Meulemans et al., 2003; Andrés et al., 2008). The poor accuracy of such reference methods may be attributable to heterogeneity of meat samples, variability in spectrum wavelengths, and/or the techniques used for spectra acquisition. Such variation can adversely affect the results achievable when these traits are studied (Prieto et al., 2009). Good predictions for DL and CL have been reported only in one study on pork ($R^2 = 0.71$; Forrest et al., 2000) and one on beef ($R^2 = 0.86$; Ripoll et al., 2008) meat. We also found that NIRS was limited in ability to predict SF ($R^2 = 0.21$), confirming previous findings in beef (Leroy et al., 2003; Andrés et al., 2008), pork (Chan et al., 2002), and poultry (Liu et al., 2004). This may be attributable to the use of homogenized samples, a sub-optimal spectrum wavelength, and/or limited variation in the available reference data for SF.

Variance components and heritability

Point estimates (medians of the marginal posterior density of each parameter) for the additive genetic and residual SD of BQ traits measured by reference methods and predicted by

NIRS are shown in Table 2. The additive genetic and residual SDs were always lower for the predicted than measured BQ traits, even if the difference varied greatly according to the specific trait.

The median of the marginal posterior density of the difference (loss of variability) between the genetic SD for L^* measured and predicted by NIRS ($\Delta\sigma_A$) was -25%, with a posterior probability of being lower than zero (P) close to 100%. A similar result was observed for a^* , with a $\Delta\sigma_A$ of -20%, whereas reductions in genetic variability were much less pronounced for b^* , H , and SI ($\Delta\sigma_A < 10\%$). The loss of genetic variability caused by NIRS estimation was $\geq 60\%$ for SF , DL , and CL . The loss of residual variation ($\Delta\sigma_E$) was generally similar to $\Delta\sigma_A$, with the exception of b^* and SI , which showed higher phenotypic losses.

A study on milk coagulation properties measured using a reference method and predicted by infrared spectroscopy showed that both additive genetic and residual SDs were lower when estimated from infrared-based predictions, with average $\Delta\sigma_A$ and $\Delta\sigma_E$ values being -14% and -27%, respectively, for rennet coagulation time, and -6% and -37%, respectively, for curd firmness (Cecchinato et al., 2009). These findings are similar to those observed for color traits in the present work. Considering all traits together, the losses of phenotypic, additive genetic, and residual SD caused by NIRS prediction is strictly associated with the R^2 values of the calibration equations (Figure 1).

Features of the marginal posterior distributions of heritability of BQ measured and predicted by NIRS are shown in Table 3. Point estimates of heritability for BQ measures differed principally when color-related traits were examined, ranging from 0.13 to 0.63. The heritabilities of L^* and a^* were moderate, and in agreement with previous estimates (Aass, 1996; Johnston et al., 2003). Saturation index and b^* showed the lowest estimates of heritability (0.15 and 0.13,

respectively), whereas H was the most heritable trait (0.63). Point estimates of heritability were low for CL (0.05) and SF (0.10), and moderate to low for DL (0.24). Only a few studies have investigated genetic aspects of water-holding capacity, and the results were contradictory, with heritability estimates for CL of 0.25 (Riley et al., 2002), 0.15 (Johnston et al., 2003), and 0.01 (Cecchi et al., 2003). We found that the heritability estimate for SF was 0.10, similar to that reported by Riley et al. (2003), but lower than the values obtained by Splan et al. (1998), Wheeler et al. (2001a), and Dikeman et al. (2005).

Heritability estimates for BQ predicted by NIRS were similar to or larger than estimates for measured BQ, except for L* and DL. Considering all BQ traits, heritabilities of measured and predicted traits showed a correlation of 0.78. When we compared the statistics in Table 1 with the estimates in Table 3, we found that neither the absolute value of heritability of predicted BQ traits nor the difference between heritabilities of the predicted and measured values was directly linked to the R^2 value of the NIRS calibration. The largest variations between values of heritability estimated using measured and predicted traits were observed for b* (0.13 to 0.29), CL (0.05 to 0.17), DL (0.24 to 0.14), and SI (0.15 to 0.23). These traits also exhibited the largest differences between $\Delta\sigma_A$ and $\Delta\sigma_E$ (Table 2).

Correlations between measured and predicted beef quality traits

Point estimates (posterior medians) and lower and upper bounds of the 95% highest posterior density intervals (HPD95) for additive genetic (r_A) and phenotypic (r_P) correlations between measured and predicted BQ traits are shown in Table 4. The estimates were much higher for genetic than for phenotypic correlations, with the exception of CL. The genetic correlation for DL was fairly high (0.72), although the phenotypic correlation (0.24) and R^2 of

the calibration equation (0.17) were low. For all color traits, the estimates between predicted and measured traits were very high and ranged from 0.85 (L*) to 0.99 (H). The estimated posterior densities of the genetic correlations between measures and predictions of BQ were skewed (data not shown), and similar among all color traits. The estimated symmetric 95% posterior density regions for color aspects showed that, in the least favorable situation (L*), the genetic correlation between measured and predicted values had a 97.5% posterior probability of being > 0.53 (data not shown). The lower boundary of the highest 95% posterior density interval was much lower for DL than for color values, but the probability of the genetic correlation of being greater than zero was 98% (data not shown).

The additive genetic correlation between predicted and measured BQ traits was the most important criterion for using NIRS-based predictions as indicator traits in breeding programs (Cecchinato et al., 2009; Rutten et al., 2010). Considering all the BQ traits, the additive genetic correlations exhibited a very low relationship with heritabilities of predicted traits (Figure 2). A comparison of CL and DL is particularly significant, in that these parameters showed similar heritabilities of predicted values (0.17 and 0.14, respectively), but completely different additive genetic correlations between predicted and measured values (-0.04 and 0.72, respectively).

The additive genetic correlations seemed to be positively correlated with the R^2 values of the calibration equations ($R^2 = 0.67$), but a comparison between CL and DL makes clear the range of possible variations. The R^2 value of the calibration equation was much more directly correlated with the phenotypic correlation between predicted and measured BQ values ($R^2 = 0.94$) than with the genetic correlation.

To the best of our knowledge, this study is the first one dealing with the use of NIRS to assess indicator traits in a breeding program for enhanced BQ. Our findings indicate that,

although the R^2 values of some calibration equations were low, the additive genetic correlations between predicted and measured values of BQ remained quite high. As the use of NIRS calibration equations resulted in losses of additive genetic and phenotypic variability in an unpredictable manner, the heritability estimates of predicted values may be higher or lower than those of the measured values. Thus, the heritability of predictions alone cannot be considered a good indicator of the suitability of a calibration equation. A combination of R^2 values of calibration, heritability of predicted values, and loss of phenotypic variability, is required to determine the utility of the technique used. This is particularly important if the available database of predicted and measured values is not large enough to directly estimate additive genetic correlations between measures and predictions traits. Our findings support the possibility of using NIRS spectra and calibration equations to genetically improve color traits, whereas DL, CL, and SF need to be investigated using larger datasets.

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Table 1. Descriptive statistics of beef quality (BQ) traits for the calibration set (n = 268) and test set (n = 940)^a

Item ^b	Calibration set							Test set			
	Mean	CV, %	Minimum	Maximum	R ^{2c}	RMSEC ^d	RER ^e	Mean	CV, %	Minimum	Maximum
L*	34.28	10.33	27.36	44.54	0.64	2.12	8.10	34.67	9.76	21.08	37.46
a*	16.46	15.38	9.45	22.69	0.68	1.41	9.39	16.39	15.77	12.96	27.71
b*	14.85	14.89	9.39	20.92	0.44	1.65	6.99	15.09	14.60	8.85	20.68
H	42.21	9.26	32.61	53.19	0.81	1.69	12.18	42.63	8.60	29.79	54.19
SI	22.28	13.64	15.04	31.03	0.59	1.94	8.24	22.36	13.94	14.51	30.94
DL, %	3.98	33.23	1.46	8.05	0.17	1.19	5.53	4.28	32.58	1.37	9.04
CL, %	24.33	14.94	13.72	32.01	0.04	3.55	5.15	24.22	14.38	12.65	33.22
SF, kg	2.65	20.55	1.57	4.41	0.21	0.48	5.92	2.68	20.84	1.51	4.48

^aCalibration set: samples used to develop a calibration equation to predict BQ phenotypes using NIRS spectra; test set: independent sample used to validate the calibration equation and to estimate heritabilities and genetic correlations for measured BQ and their predictions obtained from NIRS spectra and calibration equation.

^bSF = shear force; CL = cooking loss; DL = drip loss; L* = lightness; a* = redness; b* = yellowness; H = hue angle [$H = \tan^{-1}(b^*/a^*)$];

SI = saturation index ($SI = \sqrt{a^{*2} + b^{*2}}$).

^cCoefficient of determination of calibration.

^dRoot mean square error of calibration.

^eRatio performance deviation.

Table 2. Posterior median (SD) for additive genetic (σ_A) and residual (σ_E) standard deviation of beef quality (BQ) traits measured and predicted by near-infrared spectroscopy (NIRS)

Item ^a	σ_A				σ_E			
	Measures	Predictions	$\Delta \sigma_A, \%$ ^b	P^c	Measures	Predictions	$\Delta \sigma_E, \%$ ^d	P^c
L*	1.66 (0.28)	1.25 (0.24)	-25	93.7	2.48 (0.17)	2.09 (0.14)	-16	98.6
a*	1.17 (0.20)	0.94 (0.14)	-20	94.0	1.70 (0.13)	1.24 (0.09)	-27	99.7
b*	0.64 (0.18)	0.60 (0.12)	-6	60.5	1.63 (0.07)	0.94 (0.07)	-42	100
H	2.37 (0.21)	2.16 (0.21)	-9	93.7	1.81(0.24)	1.69 (0.24)	-7	73.2
SI	0.95 (0.24)	0.92 (0.20)	-3	55.9	2.26 (0.11)	1.68 (0.10)	-26	99.9
DL, %	0.61 (0.15)	0.16 (0.04)	-74	99.6	1.07 (0.07)	0.40 (0.02)	-62	100
CL, %	0.65 (0.30)	0.18 (0.05)	-72	95.3	2.70 (0.09)	0.40 (0.02)	-85	100
SF, kg	0.15 (0.05)	0.06 (0.02)	-60	92.1	0.46 (0.02)	0.18 (0.01)	-61	100

^aSF = shear force; CL = cooking loss; DL = drip loss; L* = lightness; a* = redness; b* = yellowness; H = hue angle [$H = \tan^{-1}(b^*/a^*)$];

SI = saturation index ($SI = \sqrt{a^{*2} + b^{*2}}$).

^bMedian of the marginal posterior density of the difference between the genetic standard deviations of BQ measured and predicted by NIRS.

^cPosterior probability for values of the difference lower than zero.

^dMedian of the marginal posterior density of the difference between the residual standard deviations of BQ measured and predicted by NIRS.

Table 3. Features of the marginal posterior distributions of heritability of beef quality (BQ) traits measured and predicted by near-infrared spectroscopy (NIRS)

Item ^a	h ² Measures			h ² Predictions		
	Median ^b	HPD95 ^c	<i>P</i> (h ² > 0.10) ^d	Median ^b	HPD95 ^c	<i>P</i> (h ² > 0.10) ^d
L*	0.31	0.06; 0.47	99.9	0.26	0.05; 0.34	99.6
a*	0.32	0.14; 0.57	99.9	0.36	0.17; 0.43	100
b*	0.13	0.03; 0.30	67.7	0.29	0.10; 0.52	97.8
H	0.63	0.45; 0.85	100	0.62	0.43; 0.86	100
SI	0.15	0.04; 0.33	81.8	0.23	0.08; 0.45	95.7
DL, %	0.24	0.05; 0.47	93.8	0.14	0.05; 0.32	71.3
CL, %	0.05	0.01; 0.20	24.2	0.17	0.05; 0.40	83.7
SF, kg	0.10	0.01; 0.28	49.0	0.10	0.02; 0.24	47.2

^aSF = shear force; CL = cooking loss; DL = drip loss; L* = lightness; a* = redness; b* = yellowness; H = hue angle [$H = \tan^{-1}(b^*/a^*)$]; SI = saturation index ($SI = \sqrt{a^{*2} + b^{*2}}$).

^bMedian of the marginal posterior density of the parameter.

^cHighest posterior density region at 95%.

^dPosterior probability for values of h² greater than 0.10.

Table 4. Posterior median and bounds of the 95% high posterior density region (HPD95) for the genetic (r_A) and phenotypic (r_p) correlations between beef quality (BQ) traits measured and predicted by near-infrared spectroscopy (NIRS)

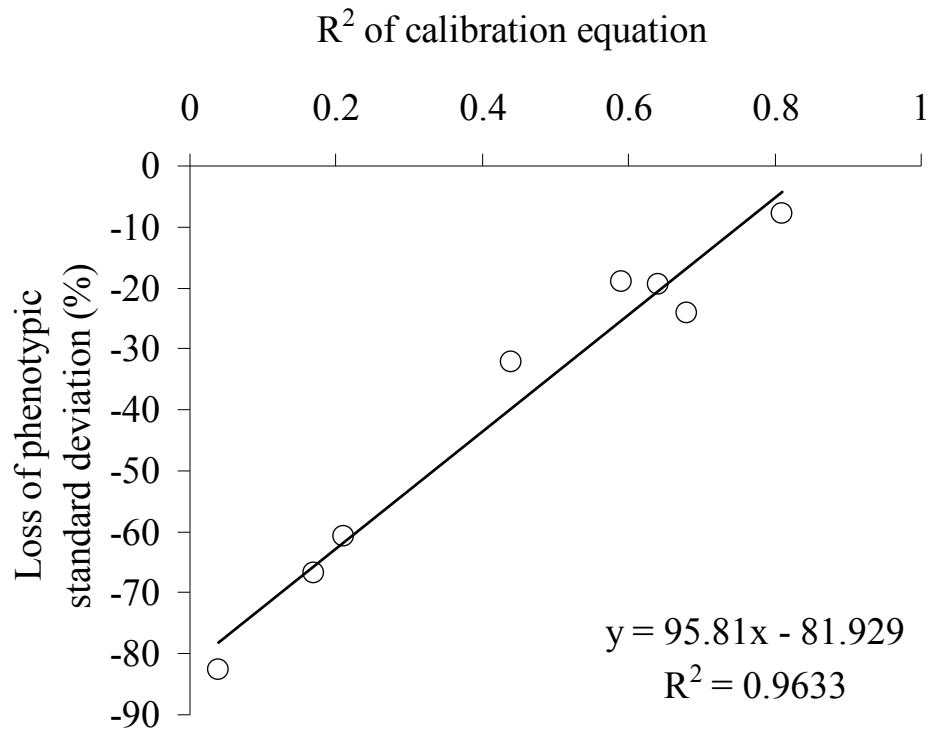
Correlation ^a	r_A		r_p	
	Median ^b	HPD95 ^c	Median	HPD95
L* with pL*	0.85	0.53; 0.98	0.60	0.55; 0.65
a* with pa*	0.98	0.83; 0.99	0.67	0.62; 0.71
b* with pb*	0.93	0.44; 0.99	0.47	0.38; 0.54
H with pH	0.99	0.96; 0.99	0.76	0.72; 0.79
SI with pSI	0.95	0.61; 0.99	0.61	0.55; 0.66
DL with pDL	0.72	-0.07; 0.98	0.24	0.17; 0.32
CL with pCL	-0.04	-0.83; 0.84	0.04	-0.03; 0.11
SF with pSF	-0.10	-0.85; 0.86	0.02	-0.05; 0.09

^aSF = shear force; pSF = shear force predicted by NIRS; CL = cooking loss; pCL = cooking loss predicted by NIRS; DL = drip loss; pDL = drip loss predicted by NIRS; L* = lightness; pL* = lightness predicted by NIRS; a* = redness; pa* = redness predicted by NIRS; b* = yellowness; pb* = yellowness predicted by NIRS; H = hue angle [$H = \tan^{-1}(b^*/a^*)$]; pH = hue angle predicted by NIRS; SI = saturation index ($SI = \sqrt{a^{*2} + b^{*2}}$); pSI = saturation index predicted by NIRS.

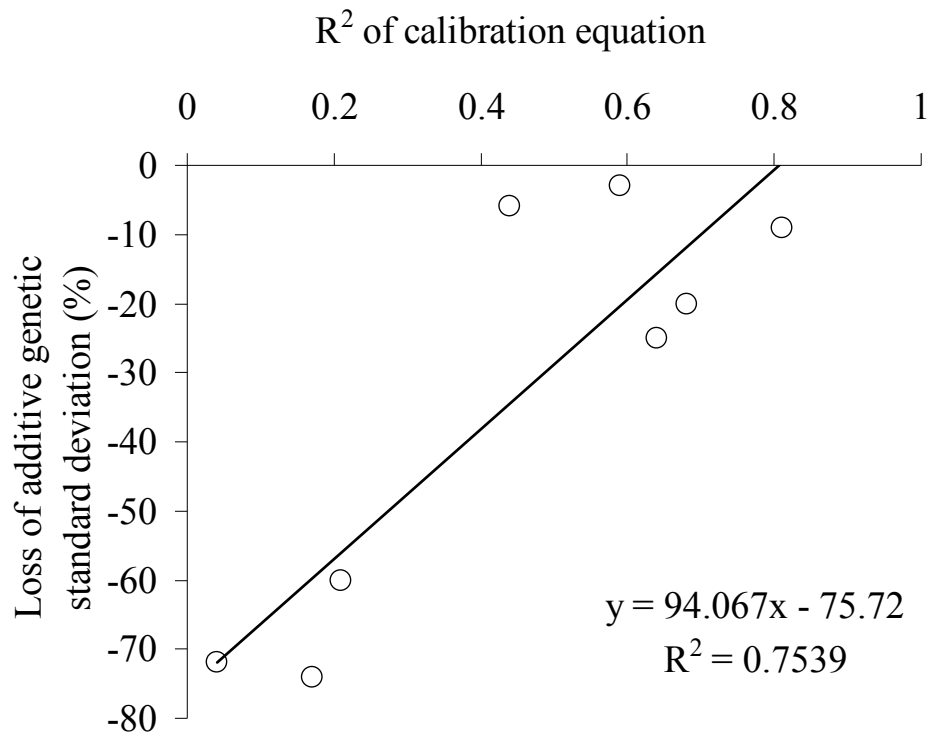
^bMedian of the marginal posterior density of the parameter.

^cHighest posterior density region at 95%.

Figure 1
[a]



[b]



[c]

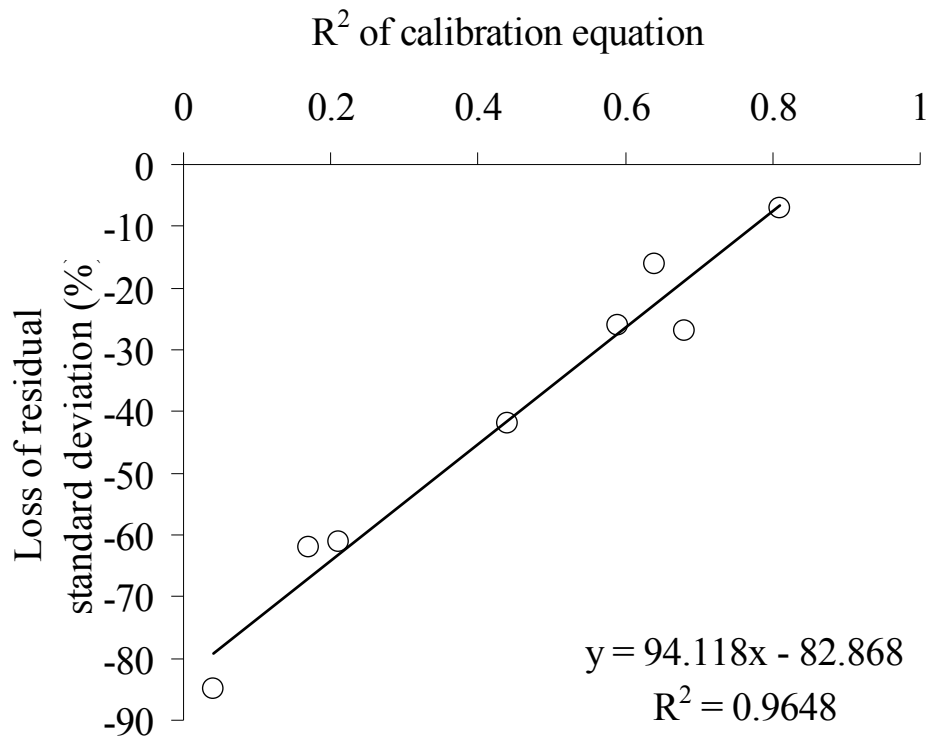
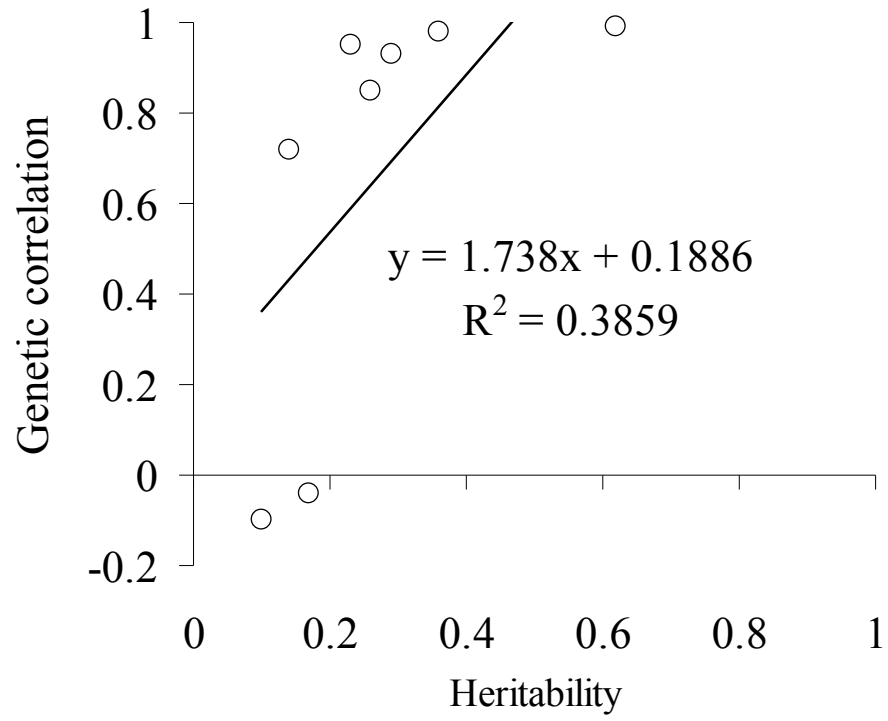


Figure 2
[a]



[b]

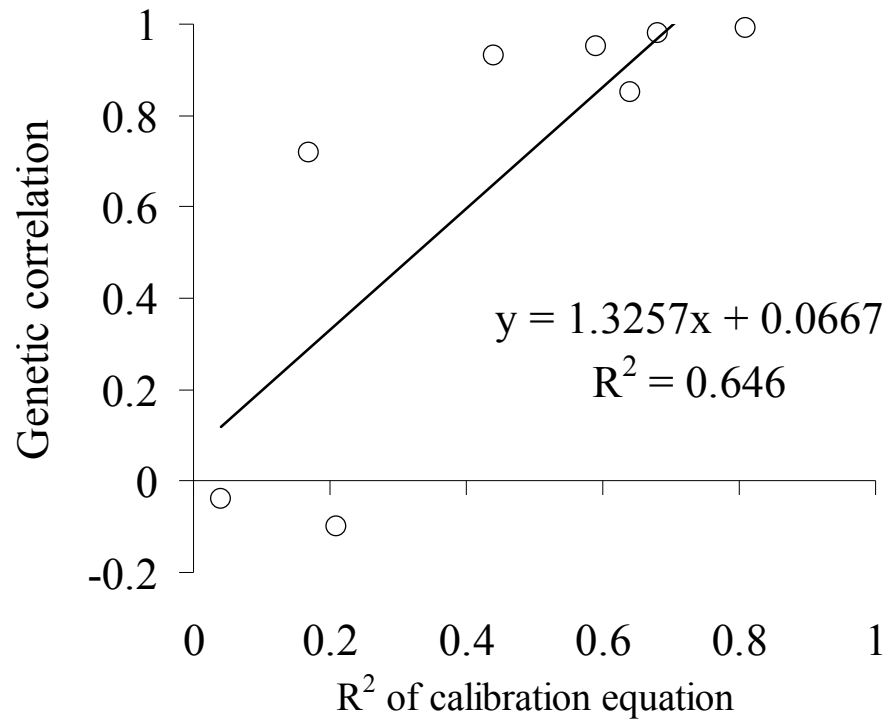


Figure 1. Relationships between losses of [a] phenotypic, [b] additive genetic, and [c] residual standard deviation of beef quality (BQ) traits predicted by near-infrared spectroscopy (NIRS) and coefficient of determination (R^2) of each calibration equation^a.

^a BQ traits: SF = shear force; CL = cooking loss; DL = drip loss; L* = lightness; a* = redness; b* = yellowness; H = hue angle [$H = \tan^{-1}(b^*/a^*)$]; SI = saturation index

Figure 2. Relationships of genetic correlations between measured and predicted BQ traits with [a] heritabilities of predicted traits and [b] coefficient of determination (R^2) of each calibration equation.

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