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J ANIM SCI 2011, 89:2687-2695.

doi: 10.2527/jas.2010-3740 originally published online March 31, 2011

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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 Piedmontese bulls ($n = 1,230$) were raised and fattened on 124 farms and slaughtered at the same commercial abattoir. The BQ traits evaluated were shear force (SF, kg), cooking loss (CL, %), drip loss (DL, %), lightness (L^*), redness (a^*), yellowness (b^*), saturation index (SI), and hue angle. Near-infrared spectra were collected using a Foss NIRSystems 5000 instrument 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 regressions, followed by application of these models to the validation subset ($n = 940$). Estimations of (co)variance for measures of BQ and NIRS-based predictions were ob-

tained 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^* ($R^2 = 0.68$), hue angle ($R^2 = 0.81$), and saturation index ($R^2 = 0.59$), but not for b^* , DL, CL, and SF. The loss of additive genetic variance of predicted vs. measured L^* , a^* , DL, CL, and SF was generally high and was 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 were greater 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 indicator traits to improve meat quality of the Piedmontese breed.

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

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J. Anim. Sci. 2011. 89:2687–2695
doi:10.2527/jas.2010-3740

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). Because 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. Because 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; Hildrum et al., 1995). Conversely, near-infrared spectroscopy (NIRS) is less reliable in predicting technological variables of meat and meat products (Abeni 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 be-

¹The authors thank the Italian Ministry of Agriculture (MIPAAF, Rome, Italy) for financial support and the National Association of Piemontese Breeders (ANABoRaPi, Carrù, Italy) for supplying pedigree information.

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Received November 28, 2010.

Accepted March 21, 2011.

tween 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

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from an existing database; the analyzed records were collected after slaughtering of animals in a commercial abattoir (Carrù, Piemonte, Italy) from March 2005 to February 2007. The authors did not have direct control over the care of the animals included in this study.

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, 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 (1 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) in a portable cooler (4°C). On arrival, samples were stored at 4°C in a chilling room until measurement of BQ traits.

Physical Analysis and NIRS

After aging for 8 d, the 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 was 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^* (lightness), a^* (redness), b^* (yellowness)] of CIE

(1976) were measured at 5 random positions. Saturation index (**SI**) was calculated using the formula $SI = \sqrt{a^{*2} + b^{*2}}$, whereas hue angle (**HA**) was calculated from the formula $HA = \tan^{-1}(b^*/a^*)$ (AMSA, 1991). The variables L^* , a^* , b^* , SI, and HA were measured 5 times each, and the measures were averaged before 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 CL (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 5 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, by 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/s). Both CL and SF were measured 5 times each, and measures were averaged before statistical analysis.

Near-infrared spectra were collected on fresh minced samples using a Foss NIRSystems 5000 instrument (FOSS NIRSystems Inc., Laurel, MD) 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 before data analysis.

Statistical Analysis

Validation Procedure. The original data set 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 the calibration equations based on NIRS spectra, a holdout validation procedure was carried out. This method involved the partition of data into 2 subsets, a calibration and a test subset. The former was used to develop a calibration equation that could predict individual BQ phenotypes by using NIRS spectra, whereas the latter was employed to validate the calibration equation and to estimate heritabilities and genetic correlations for the 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 regressions (Unscrambler software, 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; Dal Zotto et al., 2008; De Marchi et al., 2009).

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 less than 3 have little practical utility; RER values between 3 and 10 indicate the models are limited to good practical utility; and RER values above 10 indicate a 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 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 8 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 wk), 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:

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

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 2×2 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

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

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

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

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

where \mathbf{P}_1 is a 2×2 herd (co)variance matrix and \mathbf{P}_2 is a 2×2 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 autocorrelated 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, it was 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, 1 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 the 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 SE (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

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

Item ²	Calibration set ³							Test set			
	Mean	CV, %	Minimum	Maximum	R ²	RMSEC	RER	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
HA	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

¹Calibration set = samples used to develop a calibration equation to predict BQ phenotypes using near-infrared 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 near-infrared spectra and the calibration equation.

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

³R² = coefficient of determination of calibration; RMSEC = root mean square error of calibration; RER = ratio performance deviation.

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

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

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

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

RESULTS AND DISCUSSION

The Piedmontese (Piemontese), the most important Italian beef cattle breed, is characterized by muscular

hypertrophy (Kambadur et al., 1997) and is actively selected for traits such as daily BW 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., 2010) and BQ traits (Destefanis et al., 2003; Schiavon et al., 2011) 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

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

Item ¹	σ_A				σ_E			
	Measures	Predictions	$\Delta\sigma_A$, ² %	P ³	Measures	Predictions	$\Delta\sigma_E$, ⁴ %	P ³
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
HA	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

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

²Median of the marginal posterior density of the difference between the genetic SD of BQ measured and predicted by NIRS.

³P = posterior probability for values of the difference less than zero.

⁴Median of the marginal posterior density of the difference between the residual SD of BQ measured and predicted by NIRS.

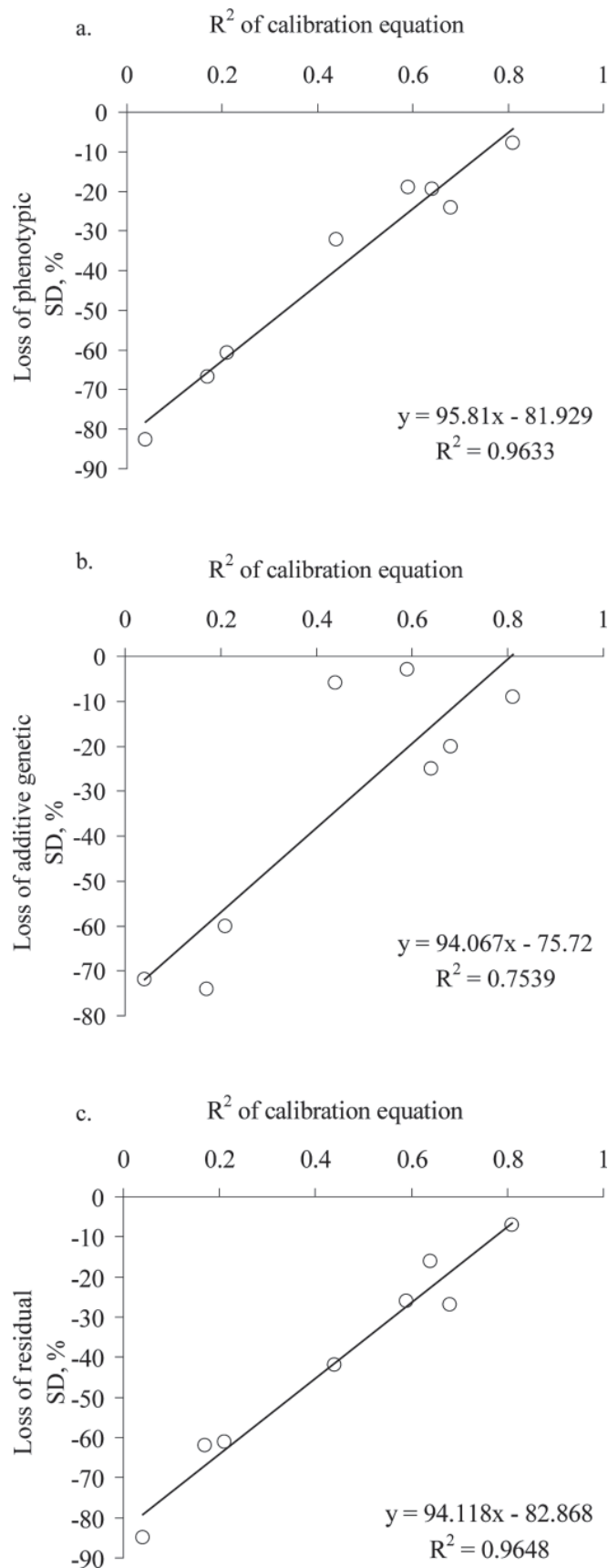


Figure 1. Relationships between losses of a) phenotypic, b) additive genetic, and c) residual SD of beef quality (BQ) traits (shear force, cooking loss, drip loss, lightness, redness, yellowness, hue angle [$HA = \tan^{-1}(b^*/a^*)$], saturation index) predicted by near-infrared spectroscopy and the coefficient of determination (R^2) of each calibration equation.

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 CV of BQ traits in the 2 subsets were similar. The CV were quite large and ranged from 9.26 (HA) 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 small ($R^2 < 0.25$) for DL, CL, and SF (Table 1). The RMSEC 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 RER values varied from 5.15 (CL) to 12.18 (HA), showing limited to good practical utility of the prediction models. Except for b^* , the R^2 values of all color indices were quite large (0.59 to 0.81), indicating that NIRS could predict these traits satisfactorily (Williams, 2003). The 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 were more accurate than the 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 the heterogeneity of meat samples, the variability in spectrum wavelengths, the techniques used for the acquisition of spectra, or all 3. 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 in only 1 study on pork ($R^2 = 0.71$; Forrest et al., 2000) and in only 1 study on beef ($R^2 = 0.86$; Ripoll et al., 2008). We also found that NIRS was limited in its 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 suboptimal spectral wavelength, limited variation in the available reference data for SF, or all 3.

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 SD were always less for the predicted than the measured BQ traits, even though the difference varied greatly according to the specific trait.

Table 3. Features of the marginal posterior distributions of heritability of beef quality (BQ) traits measured and predicted by near-infrared spectroscopy (NIRS)¹

Item ²	h ² measures			h ² predictions		
	Median	HPD95	<i>P</i> (h ² > 0.10)	Median	HPD95	<i>P</i> (h ² > 0.10)
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
HA	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

¹Median = median of the marginal posterior density of the parameter; HPD95 = highest posterior density region at 95%; *P* = posterior probability for values of h² greater than 0.10.

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

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 less 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*, HA, 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 that of $\Delta\sigma_A$, with the exception of b* and SI, which showed greater 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 SD were less 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 (Cec-

chinato 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 are strictly associated with the R² 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 were in agreement with previous estimates (Aass, 1996; Johnston et al., 2003). Saturation index and b* showed the smallest estimates of heritability (0.15 and 0.13, respectively), whereas HA was the most heritable trait (0.63). Point estimates of heritability were low for CL (0.05) and SF (0.10) and were moderate to low for DL (0.24). Only a few studies have investigated genetic aspects of water-

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)¹

Correlation ²	<i>r_A</i>		<i>r_p</i>	
	Median	HPD95	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
HA with pHA	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

¹Median = median of the marginal posterior density of the parameter; HPD95 = highest posterior density region at 95%.

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

holding capacity, and the results have been contradictory, with heritability estimates for CL of 0.25 (Riley et al., 2003), 0.15 (Johnston et al., 2003), and 0.01 (Cecchi et al., 2004). We found that the heritability estimate for SF was 0.10, similar to that reported by Riley et al. (2003) but less 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 the 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 BQ Traits

Point estimates (posterior medians) and lower and upper bounds of the 95% highest posterior density intervals for additive genetic and phenotypic correlations between measured and predicted BQ traits are shown in Table 4. The estimates were much greater 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 (HA). The estimated posterior densities of the genetic correlations between measures and predictions of BQ were skewed (data not shown), and were 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 less for DL than for color values, but the probability of the genetic correlation 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 the 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 clarifies 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.

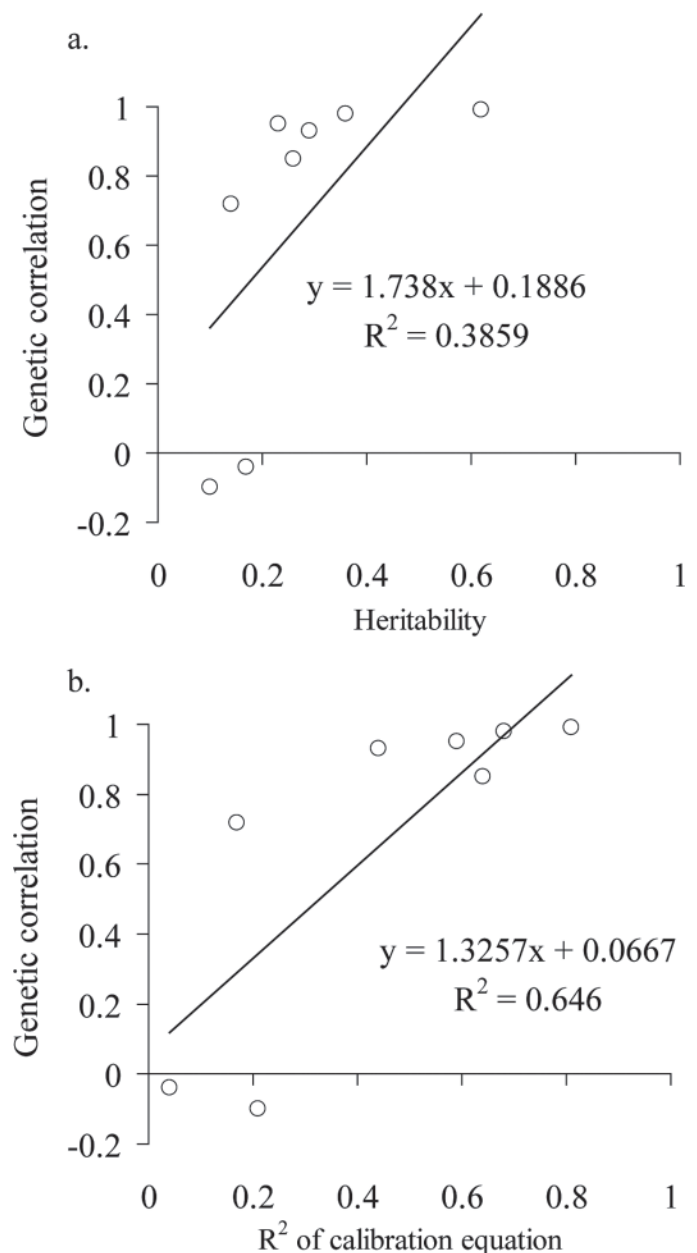


Figure 2. Relationships of genetic correlations between measured and predicted beef quality (BQ) traits (shear force, cooking loss, drip loss, lightness, redness, yellowness, hue angle [$HA = \tan^{-1}(b^*/a^*)$], saturation index) with a) heritabilities of the predicted traits and b) the coefficient of determination (R^2) of each calibration equation.

To 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. Because 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 greater or less 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 the R^2 values of calibration, the heritability of predicted values, and the 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 measured and predicted 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 data sets.

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