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Highlights

- Carcass and beef quality traits are heritable in the Piemontese breed.

- Genetic and phenotypic correlations among beef quality traits often differ.

- Some quality traits are indirectly modified by selection for growth rate and muscularity.

Abstract

Age at slaughter (AS), carcass weight (CW), carcass daily gain (CDG), conformation (EUS), and rib-eye area (REA) were recorded on 1,166 Piemontese young bulls. pH, lightness (L*), redness (a*), yellowness (b*), hue angle (h*), chroma (C*), purge loss (PL), cooking loss (CL) and shear force (WBSF) were assessed on the *Longissimus thoracis* muscle of the same animals. Heritability of carcass traits ranged from 0.07 (EUS) to 0.32 (CDG), with those of meat quality from 0.12 (PL) to 0.32 (WBSF). Genetically, an increase in AS exerts an unfavourable effect on PL (0.40) and colour traits (L*-0.20, a*-0.32, b* -0.25), whereas CW and CDG have the opposite effect. EUS is correlated favourably with PL (-0.32) and unfavourably with WBSF (0.53), while REA is correlated unfavourably with PL (0.41), CL (0.35), a* (-0.58) and b* (-0.44), and favourably with L* (0.41). Current selection goals of the Piemontese breed can indirectly modify some of the quality traits of beef, particularly colour and tenderness.

Keywords: heritability, meat colour traits, tenderness, cooking losses, carcass traits, Piedmontese.

1. Introduction

Beef consumption in the EU has declined over the last 20 years by 12% (Organisation for Economic Co-Operation and Development, 2017). Together with adverse publicity concerning environmental, health, authenticity and safety issues, inconsistent quality may have contributed to this decline (Farmer & Farrell, 2018). Consumers want beef that is safe, nutritious and of good eating quality (Verbeke et al., 2010) and would be willing to pay a higher price for better eating quality if this can be assured (Polkinghorne & Thompson, 2010).

Knowledge of meat quality characteristics is therefore essential for the beef market (Farmer & Farrell, 2018), and how they evolve over time is crucial for the future of many beef production systems. However, as the operations for obtaining phenotypes at the population level are expensive and laborious, it is very rare for measurements or sensory scores (Gill et al., 2010; Do et al., 2016) of meat quality traits to be directly used in the selection of specialised beef breeds.

In order to understanding the direction meat quality will take based on current selection goals, knowledge of the genetic relationships between meat quality traits and the traits under improvement in beef cattle genetic programmes is required.

To reduce the generation interval while maintaining a good level of selection accuracy, beef breeds are mainly selected according to production traits collected on candidate sires during on-station performance testing (Andersen et al., 1981). Production traits (daily gain, live fleshiness) are used as predictors of carcass traits, which, being difficult to collect at the slaughterhouse, are rarely available and hence rarely used (Johnston, Reverter, Ferguson, Thompson, & Burrow, 2003).

Several studies have quantified the heritability of certain measured or scored meat quality traits in cattle breeds reared in very different farming and market systems (Wolcott et al., 2009; Gill et al., 2010; Rolf et al., 2015; Do et al., 2016) and have shown the existence of genetic variability among these traits that may be exploited for genetic improvement.

Some investigations in cattle have focussed on estimating the genetic correlations between live animal performances and meat quality traits (Marshall, 1999; Burrow, Moore, Johnston, Barendse,

& Bindon, 2001) and have found a few unfavourable relationships between growth and meat quality traits. Few results have been published on the genetic correlations between traits included in the breeding objective and meat characteristics in the European framework of specialised beef cattle breeds (Bonfatti, Albera, & Carnier, 2013). Despite the higher value of meat from hypertrophied animals (European Commission, 2011), only one attempt has been made to study the heritability of beef quality traits and their genetic correlations with production traits in a double-muscled beef breed (Boukha et al., 2011). In this study, both carcass weight and age at slaughter were considered as environmental effects and included in the model to estimate the genetic parameters of meat quality traits accordingly. As a consequence, the estimated heritabilities of meat quality traits were obtained at equal carcass weights and ages. However, given the genetic variability in weight and age at slaughter, further knowledge of their relationships with meat quality traits is needed in order to obtain unbiased predictions of breeding values (Sbarra, Mantovani, Quaglia, & Bittante, 2013).

The aim of this study, then, was to investigate the genetic parameters and to analyse the phenotypic and genetic relationships within and between carcass and meat quality traits.

2. Material and Methods

2.1. Animals and beef sampling

A total of 115 herds in the Piemonte region (north-west Italy) operating 6 different farming systems, from very traditional to more intensive, were selected for this study. They belonged to the six main production systems identified in the Piemontese breed according to operation cycle, housing system, feed supply and feed distribution (Savoia et al., 2019). Herds characterised by restricted feeding without the use of total mixed ration (TMR) were classified as traditional systems, with a distinction made between tie-stall and loose-housing of animals. Modern systems, characterised by loose-housed animals fed ad libitum, were splitted into those using or not TMR, and further differentiated according to being cow-calf operations or specialised fatteners. Their

clustering and selection criteria, together with the feeding regime and fattening conditions of animals were described in details by Savoia et al. (2019).

The study was carried out on 1,327 Piemontese young bulls reared on the aforementioned commercial herds and slaughtered on the herd owners' decision at the same commercial abattoir (Operti, Centallo [CN], Italy) from April 2015 to February 2017. The young bulls selected were sired by 204 A.I. purebred sires on 1,286 dams, all registered in the Italian Piemontese Herd Book.

After slaughter, hot carcass weight (CW) and carcass conformation class according to the EU linear grading system (Commission of the European Communities, 1982) were recorded. In order to obtain more detailed differentiation of carcass conformation, the six main grades (S, E, U, R, O, P, from the best to the worst) were each subdivided into three subclasses (+, = or -). Prior to statistical analysis, the categories of carcass conformation were converted into numerical scores (EUS) ranging from 1, corresponding to the P- class, to 18, corresponding to the S+ class. Fatness was not scored in this study because of the lack of variation in this attribute due to the well-known leanness of the carcasses of double-muscled breeds, which in turn is due to local market demands. Age at slaughter (AS) was calculated from the date of birth to the date of slaughter. As the individual live weights of the animals were unavailable, carcass daily gain was used (CDG), calculated as the ratio of carcass weight to age at slaughter, as a measure of the young bulls' growth rate (Juniper et al., 2005; Boukha et al., 2011). The carcasses were not electrically stimulated and were chilled at 4 °C for twenty-four hours *post-mortem*.

Twenty-four hours after slaughter, individual samples (4.0 cm thick) of the *Longissimus thoracis* (LT) muscle were taken from between the fifth and sixth thoracic vertebrae. These beef samples were scanned with an HP Scanjet 5590 Digital Flatbed Scanner (Hewlett-Packard, Palo Alto, California) to obtain images from which to measure the rib-eye area (REA, cm^2) and were then individually vacuum-packaged and transferred under refrigerated conditions to the laboratory. Upon arrival, samples were stored at 4°C in a chilling room for 6 days before measuring the meat quality traits (at 7 days *post-mortem*).

2.3. Analysis of Meat Quality Traits

As described in detail in a previous study (Savoia et al., 2019), the following meat quality characteristics were analysed after ageing (at 7 days *post-mortem*):

- purge losses (PL, %) were determined as the difference between weight at packaging and weight after ageing;

- ultimate pH was measured using a portable Crison PH 25+ pH meter (Crison Instruments S.A., Alella, Barcelona, Spain) equipped with a Crison 52 32 glass electrode suitable for meat penetration and an automatic temperature compensator (Boccard et al. 1981);

- rib eye area (REA, cm^2) was measured from the digital images of the processed samples using the Image Pro Plus 4.5.1. software (Media Cybernetics, 2001);

- colour traits were measured on the freshly-cut surface of the steak after 1 h of blooming at 4 °C using a Konica Minolta CR-331C colorimeter (Konica Minolta Sensing Americas Inc., Ramsey, NJ, USA) and recorded in terms of CIELAB coordinates (CIE 1976): lightness (L*), redness (a*) and yellowness (b*); hue angle (h*) was calculated as h* $= \tan^{-1}(b^*/a^*)$, chroma (C*) as C* = (a*^{2} + b*^{2})$^{0.5}$. Three random readings at different locations on the meat surface were taken and averaged;

- cooking losses (CL, %) were obtained by sealing the steak in a polyethylene bag and cooking in a water bath preheated at 75 °C to an internal temperature of 70 °C (Honikel, 1998);

- Warner Bratzler shear force (WBSF, N) was measured by shearing 6 cylindrical cores of cooked meat 1.27 cm in diameter with a V-shaped Warner-Bratzler blade fitted to an Instron Universal Machine model 5543 (Instron, Norwood, MA, USA) (A.M.S.A., 2015).

2.4. Statistical Analyses

Prior to statistical analysis, observations falling outside the range of three standard deviations from the mean of each carcass or quality trait were excluded from the data-set.

2.4.1. Estimation of (co)variance components and genetic parameters

(Co)variance components were estimated by REML procedures using the VCE software (version 6.0; Groeneveld, Kovac, & Mielenz, 2010). (Co)variance components for carcass and meat quality traits were estimated through multiple-trait analyses within each group of traits. (Co)variance components between the two group of traits were estimated through a series of multiple-trait analyses that included all the carcass traits and one meat quality trait at a time. The general model can be written in matrix notation as:

$$y = X\beta + W1c + W2q + Zu + e$$

where y contains the observations for carcass traits and the meat quality trait in question, β is the vector of non-genetic fixed effects, c is the vector of random herd effects (98 levels), q is the vector of the random effect of batch of slaughter (106 levels), u is the vector of animal additive genetic effects, e is the vector of random residual effects, and X, $W1$, $W2$ and Z are the incidence matrices of proper dimensions. Preliminary analyses suggested inclusion of the fixed effects of birth season (4 classes: January-March, April-June, July-September, October-December) for WBSF (N), and of parity of dam (4 classes: 1st, 2nd, 3rd-8th, >8) for carcass weight. Both these effects were included in the model for PL (%), age at slaughter and carcass daily gain.

The random effects of herd and of day of slaughter were assumed to be normally and indipendently distributed as $c \sim N(0, \ C \otimes I)$ and $q \sim N(0, \ Q \otimes I)$, where C and Q are the (co)variances matrices for herd and for day of slaughter effects respectively, and I is an identity matrix of dimension equal to the number of animals with data. A preliminary editing was performed to avoid the confounding between herd and day of slaughter effects. A minimum cell size of 3 observations was required for both the effects resulting, on average, in 11 animals from 3,8 different herds within each day of slaughter. Animal additive genetic effects were assumed to be normally distributed $u \sim N(0, \ G \otimes A)$, where G is the (co)variance matrix between animal genetic effects in the different traits and A is the numerator of Wright's relationship matrix. Additive relationships were computed using a pedigree file that included the phenotyped animals and all their known

ancestors (13,122 animals). Residuals were assumed to follow the normal distribution, $\mathbf{e} \sim N(0, \mathbf{R} I)$, where $\mathbf{R}$ is the residual (co)variance matrix and $\mathbf{I}$ an identity matrix as described above.

To facilitate comparisons with the literature estimates, we calculated intra-herd heritability as:

$$h^2 = \sigma_a^2/(\sigma_a^2 + \sigma_e^2)$$

where σ_a^2 is the additive genetic variance, σ_e^2 is the residual variance and $\sigma_a^2 + \sigma_e^2$ is equal to the intra-herd phenotypic variance. Genetic correlations were computed as:

$$r_a = (\sigma_{a1;a2})/(\sigma_{a1} \cdot \sigma_{a2})$$

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. The total phenotypic variance (σ_p^2) was defined as the sum of the herd, day of slaughter, animal and residuals variances. Phenotypic correlations were computed as:

$$r_p = (\sigma_{p1;p2})/(\sigma_{p1} \cdot \sigma_{p2})$$

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.

3. Results

3.1. Heritability of carcass and meat quality traits

Quantification of the variance components (Table 1) revealed that slaughter batch represented a minor source of variation for carcass traits (4 to 9% of phenotypic variance) except rib-eye area (18% of variance explained by slaughter batch). The effect of fattening herd was much more variable, explaining from 6% of phenotypic variance for rib-eye area to 52% for age at slaughter. The additive genetic variance represented a proportion of phenotypic variance ranging from 6% in the case of the SEUROP score and 22% for carcass daily gain, resulting in an estimated intra-herd heritability that was low for muscularity (7%), medium-high for carcass daily gain (32%) and intermediate for the other traits (18 to 21%), although standard errors were large.

Unlike carcass traits, fattening herd had a small effect and slaughter batch a greater effect on all meat colour traits, while the additive genetic variance was slightly lower than 10% of phenotypic variance for all traits except lightness (23%) (Table 2). This resulted in an estimated intra-herd

heritability of about 30% for lightness and 13% for the other colour traits. The other meat quality traits were similarly characterised by small effects of fattening herd (4 to 6% of phenotypic variance), but very large effects of slaughter batch, from 14% for purge loss to more than 60% for pH (the latter exhibited very low phenotypic variance). Additive genetic variance represented 18% of phenotypic variance in the case of shear force, and about 10% for the other traits (Table 3). The resulting intra-herd heritabilities were about 15% for purge and cooking losses, and over 30% for muscle pH and shear force.

In general, the estimated variance components and related genetic parameters were characterised by moderate to large standard errors. However, their magnitude is in the expected range on the basis of the amount and the structure of data, reflecting an half-sibs design. The complexity and costs related to collecting phenotypes and analytical procedures limited the number of available phenotypes and affected the magnitude of standard errors of estimated parameters.

3.2. Phenotypic and genetic correlations among carcass traits

The phenotypic and genetic correlations among the carcass traits are summarised in Table 4. All phenotypic correlations were positive, ranging from almost null to intermediate values (+55%), except for the strong negative correlation (-66%) observed between age at slaughter and carcass daily gain.

The genetic correlations were often larger and more variable in sign than the phenotypic ones. Age at slaughter was negatively correlated not only with carcass daily gain but also with carcass weight, but positively correlated with SEUROP score and also with rib-eye area, although to a much lesser extent.

Carcass weight and carcass daily gain were positively correlated, while both were negatively correlated with SEUROP score and were independent of rib-eye area. Lastly, a negative correlation was observed between SEUROP score and rib-eye area.

3.3. Phenotypic and genetic correlations among meat quality traits

Table 5 summarises the phenotypic and genetic correlations among the meat quality traits. Among the colour traits, L* and b* were strongly correlated, as were a* and b*, both phenotypically and genetically, whereas L* and a* were independent.

Meat pH was correlated positively with shear force and cooking losses, and negatively with a* and b*. High PL (%) were associated with increased L* values, and also, although only genetically, with higher shear force and b* values and lower CL (%). Cooking losses exhibited a moderate positive genetic correlation with shear force, but a strong phenotypic correlation with a* and b*. Lastly, shear force was almost independent of colour traits.

3.4. Phenotypic and genetic correlations between carcass and meat quality traits

Phenotypic and genetic correlations between carcass traits and meat quality traits are summarised in Table 6. All phenotypic correlations were generally weak with the notable exception of the moderate positive correlations between carcass weight and a* and b*, and between carcass daily gain and L*.

The genetic correlations were generally stronger and more variable in sign. Age at slaughter exhibited moderate positive correlations with PL and shear force, but was negatively correlated with a* and b*. Both carcass weight and carcass daily gain were markedly associated with L*. Carcass weight also exhibited moderate negative correlations with pH and a positive correlation with PL. SEUROP scores were correlated negatively with PL, and positively with shear force. Lastly, rib-eye area was correlated positively with PL, CL and L*, and negatively with the a* and b* indices.

4. Discussion

4.1. Genetics of carcass traits

Savoia et al. (2019) outlined that age at slaughter of Piemontese young bulls was markedly affected by the adopted beef production system. However, the date of slaughter of the Piemontese young bulls included in this study was decided by the farmers for each individual animal. In such a situation, the age at slaughter is not only determined by "environmental" factors (herd management

and financial strategies, market requirements, etc.), but, being moderately heritable (0.18), it is also partially under the control of animal genetics. A previous study (Sbarra et al., 2013) on three non-double-muscled Italian beef breeds (Chianina, Marchigiana and Romagnola) reported h^2 values for this trait ranging from 0.28 to 0.39. Age at slaughter was therefore interpreted as a measure of slaughter/market precocity. Indeed, in farming systems where the optimal slaughtering date is decided for each animal and not on a pen/group basis, this decision is often highly affected by the live weight and fattening condition of the animals in relation to local market requirements. This interpretation is confirmed by the very low variability in carcass fatness observed in this study as assessed using the SEUROP scoring system, which did not allow genetic parameters to be estimated. In other studies focussed on estimating the genetic parameters for carcass traits, carcass fatness was either not taken into account or it produced lower heritability estimates than for the other traits (Minick, Dikeman, Pollak, & Wilson, 2004; Hornyak, Frickh, & Furst-Waltl, 2008; Gill et al., 2010; Kluska et al., 2018). So age at slaughter, although influenced by other factors as management and beef production system, could be considered an indicator of precocity in attaining optimal fat deposition and protein accretion. As fat deposition is very low and less variable in double-muscled breeds than in conventional beef breeds (Fiems, 2012), the Piemontese breed can be expected to have a lower heritability of slaughter precocity than conventional beef breeds.

The results of this study confirm carcass weight to be moderately heritable (0.19). This value falls in the interval (0.13 to 0.24) reported by Sbarra et al. (2013). In a previous study on Piemontese young bulls (Boukha et al., 2011), the heritability of carcass weight was found to be much larger (0.33), although it should be pointed out that age at slaughter was not considered a trait, as it was in our study. Instead, Boukha et al. (2011) included it in the statistical model as an "environmental" fixed factor to adjust carcass weight, and this could have led to the higher heritability they found as also confirmed by our results (data not shown). Indeed, Sbarra et al. (2013) showed that including age at slaughter in the statistical model as a covariate increased the heritability estimates of carcass weight by 4 to 6 points, but also led to biased estimation of the breeding values. The regression of carcass weight on age at slaughter does not reflect the growth

rate of an individual animal if its slaughter date is delayed, but only differences between animals of good growth potential, slaughtered earlier, and animals of lower genetic potential, slaughtered later, as evidenced by the consistent (-0.53) negative genetic correlation between age at slaughter and carcass weight and gain obtained in this study (Table 4). A similar problem regarding the age and weight of young calves sold at auction was dealt with in a previous study (Bittante, Cecchinato, Dal Zotto, De Marchi, & Penasa, 2011) and yielded similar results, because here, too, the farmer's decision to bring forward or delay sending the calf to auction was based on the expression of traits partly under genetic control (growth rate, conformation, etc.).

Almost identical levels of heritability of carcass gain, i.e. the ratio between carcass weight and age at slaughter, were found in this study (0.32), in a previous survey on the Piemontese breed (0.33) and in a study on 3 conventional beef breeds (0.27 to 0.42). As expected, carcass daily gain, being a ratio, is strongly correlated (both phenotypically and genetically, Table 4) positively with its numerator (carcass weight) and negatively with its denominator (age at slaughter).

The estimated heritability of SEUROP carcass conformation in Piemontese young bulls was poor (0.07). The Piemontese is a double-muscled breed whose muscularity is largely due to a mutation of the myostatin gene (mh: muscular hypertrophy), which is almost fixed in the population (Grobet et al., 1998; Bellinge, Liberles, Iaschi, O'Brien, & Tay, 2005). Our result is very different from the value, around 0.3, obtained in a previous study on the same breed (Boukha et al., 2011) using a different model that also included carcass weight. Adjusting carcass conformation for carcass weight increased its heritability also in our study, but still a lower value was found (0.15, data not shown). Probably the subjective nature of SEUROP scoring system is the main reason of this inconsistency between estimates. In our study, SEUROP scores of Piemontese carcasses presented modest positive phenotypic correlations with all the other carcass traits, but strong negative genetic correlations with all carcass traits except age at slaughter (which, in turn, was negatively correlated with carcass weight and gain, Table 5). The heritability value of rib-eye area was larger than that of SEUROP score, and closer to that found for carcass weight, the trait with which rib-eye area has a greater phenotypic correlation (Table 5).

There have been a large number of studies focussed on estimating the genetic parameters of carcass traits (Moser, Bertrand, Misztal, Kriese, & Benyshek, 1998; Johnston et al., 2003; Crews, Lowerison, Caron, & Kemp, 2004; Do et al., 2016), and although the results have been variable and dependent on the breeds and farming systems investigated, in most cases the genetic parameters from this study were within the range of those reported in these earlier studies.

4.2. Genetics of beef quality traits

Colour is the main quality attribute influencing consumer choice. Lightness was much more heritable than the other two colour traits, confirming the results generally found in other studies (Johnston et al., 2003). Lightness was phenotypically and genetically independent of a*, but highly correlated with b*, which in turn was highly correlated with a* (Table 5). Our results are in partial agreement with other reports in the literature, which have generally found all colour traits to be highly associated (Page, Wulf, & Schwotzer, 2001). Consistent with Boukha et al.'s (2011) findings, colour traits were independent of shear force, both genetically and phenotypically. In more extensive farming systems with conventional breeds, L* has been sometimes found to be favourably correlated with shear force (Johnston et al., 2003), and this could be because of the darker colour resulting from increased oxidative activity, often caused by pasture rearing (Dannenberger, Nuernberg, Nuernberg, & Ender, 2006). Unlike Boukha et al. (2011), we found that the genetic associations of colour traits with cooking losses were weaker than the corresponding phenotypic correlations. Our results also show that paler meat is likely to be associated with increased purge losses, especially from a genetic perspective.

Comparison with data from the literature is very difficult for these traits due to the enormous variation within and between studies with respect to breed, sex, environment, slaughter endpoint and finishing feeding regime (Johnston et al., 2003; Minick et al., 2004). With particular regard to shear force, it should be borne in mind that some aspects of the methodology (duration of ageing and data editing) can greatly affect the genetic parameter estimates (Johnston, Reverter, Robinson, & Ferguson, 2001; Zwambag et al., 2013).

The two water-holding traits, purge and cooking losses, were moderately correlated with each other and exhibited moderate positive genetic associations with shear force, indicating that better water-holding capacity is associated with tender meat. Shear force was genetically and phenotypically positively correlated with ultimate pH, and as such in the same direction - although of higher magnitude - compared with Boukha et al.'s (2011) findings, but at odds with the negative phenotypic correlation reported by Destefanis, Barge, Brugiapaglia, & Tassone (2000).

Overall, it is evident that the genetic parameter estimates for meat quality traits are largely variable in different beef cattle populations in relation to breed characteristics, the prevalent farming system and market requirements.

4.3. Effects of carcass traits on beef quality traits and perspectives for genetic improvement

The phenotypic correlations between carcass and meat traits were small, with a few exceptions regarding L*, which was correlated positively with carcass daily gain and negatively with age at slaughter, and a* and b*, which were positively associated with carcass weight (Table 6). From a genetic perspective, factors determining an increase in age at slaughter seem to have an unfavourable effect on purge losses and colour traits, whereas factors affecting carcass weight and gain have the opposite effect. These results may be explained by the negative genetic correlations between age at slaughter and carcass weight. The estimated genetic correlations between SEUROP scores and meat quality indicate that an improvement in carcass conformation may favourably affect purge losses but negatively affect meat tenderness. Lastly, the rib-eye area showed unfavourable genetic correlations with most of the meat quality traits, namely water-holding capacity and the a* and b* colour indices, whereas it was independent of shear force and favourably associated with L*.

The Piemontese breed is selected for muscularity and growth rate during on-station performance testing of candidate sires (Albera, Mantovani, Bittante, Groen, & Carnier, 2001), and for direct and maternal ease of calving during progeny testing of selected sires (Carnier et al., 2000). Traits measured with performance testing are early predictors of the true breeding goal traits, carcass

weight and gain, and SEUROP scores measured in commercial abattoirs (Albera, 2015), indeed on station live growth rate proved to be highly correlated with carcass gain from a genetic standpoint (r_g 0.87, data not shown). As the genetic correlations reported in Table 6 indicate, the current selection procedure could have a modest favourable effect on beef lightness, but an unfavourable effect on beef tenderness. Selection for maternal traits at the population level could reduce the muscularity of the cows (Bittante et al., 2018), thereby increasing sexual dimorphism, although cow muscularity is also evaluated through type scoring in the Piemontese breed (Mantovani, Cassandro, Contiero, Albera, & Bittante, 2010). A few studies have focussed on the relationships between maternal performance and carcass traits (Kluska et al., 2018) or beef production traits (Albera, Groen, & Carnier, 2004), but rarely beef quality traits.

The results obtained in this study confirm that meat quality traits are heritable and that improving them through selection is theoretically possible. Analysis of the genetic correlations also shows that the current selection of beef breeds, biased towards improving growth rate and muscularity, can indirectly modify some meat quality traits, particularly colour and tenderness. Due to the cost and the complexity of meat quality evaluation, selection for these traits based on direct phenotyping of slaughtered animals using gold standard methods is unfeasible. However, two alternative methods can be exploited for improving meat quality attributes through selection, one based on phenotypes collection, the other on genetic evaluation.

The first alternative involves predicting meat quality traits at the abattoir level by means of cheap, rapid, high-throughput methods (Farmer & Farrell, 2018). Subjective sensory evaluation has some interest, but it is complex and still expensive (Gill et al., 2010). Methods based on near-infrared spectroscopy have produced some promising results with respect to predicting meat colour and purge losses (Cecchinato, De Marchi, Penasa, Albera, & Bittante, 2011), and chemical composition and fatty acid profiles (Cecchinato et al., 2012), although results for cooking losses and tenderness have been less satisfactory (Farmer & Farrell, 2018). Most of the studies mentioned used laboratory benchtop near-infrared spectrometers requiring meat samples to be taken from the carcass (that could be depreciated). However, portable instruments have recently become available

for use in the abattoir (Craigie et al., 2010), so new research is needed to test the feasibility of selection for meat quality traits based on predictions made at the abattoir level from intact carcasses, quarters or anatomical joints.

The second alternative involves genome-wide selection based on genomic breeding values predicted from estimates of the SNP marker effects for meat quality traits. This strategy, which exploits the linkage disequilibrium between the SNP markers and the QTL affecting the investigated traits (Meuwissen, Hayes, & Goddard, 2001), requires a calibration procedure for estimating SNP effects from an "experimental" dataset to be established and subsequently used at the population level (Rolf et al., 2015). As genomic calibration needs to be repeated over time to take into account any possible weakening of the association between the SNP markers and the QTL for the traits of interest, phenotyping based on spectroscopy predictions could be coupled with a genomic approach to develop a reliable program of genetic improvement of beef quality.

5. Conclusions

The results obtained in this study show that carcass traits are heritable and that age at slaughter could be used as an indicator of slaughter precocity. Moreover, meat quality traits show that there is genetic variability which could theoretically be exploited for the genetic improvement of animals.

With a few exceptions, the correlations between carcass and meat quality traits were not phenotypically relevant, as they were in most of the cases low. From a genetic perspective, the factors determining an increase in age at slaughter seem to have an unfavourable effect on purge losses and colour traits, whereas the factors affecting carcass weight and gain have the opposite effect. These results can be explained by the negative genetic correlation between age and weight. Then, the current selection of beef breeds, based especially on improvement of growth rate and muscularity, could indirectly modify some meat characteristics, mainly those related to colour and tenderness.

Due to the cost and the complexity of collecting meat quality traits, selecting for these traits based on traditional phenotyping of slaughtered animals does not appear to be feasible. Near-

infrared spectroscopy and genomic selection seem to be possible alternatives for the genetic improvement of meat quality traits.

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Authors declare that no conflict of interest exists.

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Table 1. Descriptive statistics, variance components and heritabilities of carcass traits of Piemontese young bulls.

	Age at slaughter d	Carcass weight kg	Carcass gain kg/d	Muscularity SEUROP score (1-18)[$]	Rib-eye area cm^2
Young bulls, N	1166	1159	1161	1166	1154
General mean	539.0	438.8	0.820	14.69	92.27
Standard deviation	61.9	44.1	0.106	1.54	14.3
Minimum	382.0	309.0	0.536	10.00	52.43
Maximum	728.0	564.0	1.097	18.00	142.67
Phenotypic variance	4167	1996	0.0115	2.369	205
Variance components[a]					
- additive genetic	0.072	0.122	0.217	0.058	0.160
- day of slaughter	0.075	0.093	0.039	0.076	0.177
- herd	0.516	0.265	0.280	0.103	0.064
Intra-herd heritability[b]	0.175	0.189	0.319	0.070	0.211
SE intra-herd h^2	0.076	0.083	0.085	0.064	0.095

[a] Ratio between each variance component and the total phenotypic variance defined as the sum of the herd, day of slaughter, additive genetic and residuals variances.

[b] $\sigma_a^2/(\sigma_a^2 + \sigma_e^2)$ where σ_a^2 is the additive genetic variance, σ_e^2 is the residual variance and $\sigma_a^2 + \sigma_e^2$ is equal to the intra-herd phenotypic variance.

[$] SEUROP class with +/- subclasses converted into numerical values.

Table 2. Descriptive statistics, variance components and heritability of meat colour traits of Piemontese young bulls.

	Lightness L*	Redness a*	Yellowness b*	Chroma C*	Hue h*
Young bulls, N	1156	1157	1159	1158	1155
General mean	39.89	28.61	9.66	30.21	18.54
Standard deviation	3.49	1.74	1.66	2.15	2.03
Minimum	30.47	23.22	4.84	23.60	12.20
Maximum	50.80	33.92	14.44	36.93	23.60
Phenotypic variance	11.87	3.11	2.77	4.74	4.13
Variance components[a]					
- additive genetic	0.234	0.085	0.090	0.091	0.099
- day of slaughter	0.178	0.250	0.224	0.243	0.210
- herd	0.057	0.101	0.080	0.102	0.059
Intra-herd heritability[b]	0.306	0.132	0.129	0.139	0.135
SE intra-herd h^2	0.095	0.070	0.070	0.075	0.074

[a] Ratio between each variance component and the total phenotypic variance defined as the sum of the herd, day of slaughter, additive genetic and residuals variances.

[b] $\sigma_a^2/(\sigma_a^2 + \sigma_e^2)$ where σ_a^2 is the additive genetic variance, σ_e^2 is the residual variance and $\sigma_a^2 + \sigma_e^2$ is equal to the intra-herd phenotypic variance.

Table 3. Descriptive statistics, variance components and heritabilities of meat quality traits of Piemontese young bulls.

	pH	Purge losses %	Cooking losses %	Shear force N
Young bulls, N	1165	1155	1166	1147
General mean	5.56	4.51	16.76	41.03
Standard deviation	0.06	1.19	3.43	10.45
Minimum	5.43	1.68	7.83	15.89
Maximum	5.77	8.04	26.83	75.22
Phenotypic variance	334[c]	1.39	11.62	111
Variance components[a]				
- additive genetic	0.102	0.101	0.097	0.176
- day of slaughter	0.618	0.140	0.416	0.404
- herd	0.050	0.049	0.040	0.055
Intra-herd heritability[b]	0.308	0.124	0.179	0.325
SE intra-herd h^2	0.087	0.072	0.085	0.097

[a] Ratio between each variance component and the phenotypic variance. Ratio between each variance component and the phenotypic variance total phenotypic variance defined as the sum of the herd, day of slaughter, additive genetic and residuals variances.

[b] $\sigma_a^2/(\sigma_a^2 + \sigma_e^2)$ where σ_a^2 is the additive genetic variance, σ_e^2 is the residual variance and $\sigma_a^2 + \sigma_e^2$ is equal to the intra-herd phenotypic variance.

[c] Phenotypic variance multiplied by 10^5

Table 4. Phenotypic and genetic correlations among carcass traits of Piemontese young bulls (SE in parentheses).

	Phenotypic correlation	Genetic correlation
Age at slaughter with:		
- carcass weight	0.269 (0.061)	-0.530 (0.199)
- carcass gain	-0.663 (0.046)	-0.865 (0.066)
- SEUROP score	0.015 (0.052)	0.716 (0.188)
- rib-eye area	0.002 (0.039)	0.183 (0.107)
Carcass weight with:		
- carcass gain	0.533 (0.032)	0.883 (0.059)
- SEUROP score	0.357 (0.035)	-0.432 (0.284)
- rib-eye area	0.323 (0.038)	0.003 (0.116)
Carcass gain with:		
- SEUROP score	0.258 (0.057)	-0.653 (0.210)
- rib-eye area	0.237 (0.049)	-0.101 (0.117)
SEUROP score with:		
- rib-eye area	0.077 (0.042)	-0.539 (0.226)

Table 5. Phenotypic and genetic correlations among meat quality traits of Piemontese young bulls (SE in parentheses).

	Phenotypic correlation	Genetic correlation
Meat pH with:		
- purge losses	-0.025 (0.029)	0.002 (0.094)
- cooking losses	0.079 (0.036)	0.291 (0.093)
- shear force	0.404 (0.030)	0.450 (0.067)
- L*	-0.176 (0.038)	-0.128 (0.076)
- a*	-0.132 (0.030)	-0.549 (0.083)
- b*	-0.223 (0.033)	-0.546 (0.086)
Purge losses with:		
- cooking losses	0.110 (0.043)	-0.366 (0.128)
- shear force	0.074 (0.037)	0.262 (0.098)
- L*	0.303 (0.035)	0.775 (0.051)
- a*	-0.071 (0.037)	0.024 (0.199)
- b*	0.203 (0.036)	0.368 (0.168)
Cooking losses with:		
- shear force	0.002 (0.051)	0.299 (0.169)
- L*	-0.190 (0.049)	0.116 (0.114)
- a*	-0.803 (0.033)	-0.034 (0.067)
- b*	-0.791 (0.036)	0.057 (0.074)
Shear force with:		
- L*	0.041 (0.043)	-0.022 (0.086)
- a*	-0.141 (0.036)	0.004 (0.106)
- b*	-0.108 (0.037)	-0.008 (0.116)
L* with:		
- a*	-0.002 (0.039)	0.012 (0.156)
- b*	0.788 (0.027)	0.469 (0.110)
a* with:		
- b*	0.580 (0.007)	0.889 (0.032)

Table 6. Phenotypic and genetic correlations[1] between carcass and meat quality traits of Piemontese young bulls.

	Age at slaughter d	Carcass weight kg	Carcass gain kg/d	Muscularity SEUROP score	Rib-eye area cm^2
Phenotypic correlations:					
Meat pH	0.053	0.029	-0.023	0.030	0.003
Purge losses	-0.023	0.129	0.127	0.137	0.125
Cooking losses	-0.018	-0.031	0.005	0.012	0.043
Shear force	0.060	0.020	-0.034	0.054	0.023
L*	-0.216	0.137	0.304	0.123	0.096
a*	0.142	0.346	0.139	0.169	0.016
b*	0.064	0.348	0.213	0.197	0.061
Genetic correlations:					
Meat pH	-0.041	-0.305	-0.157	-0.113	0.143
Purge losses	0.403	0.332	-0.027	-0.316	0.668
Cooking losses	0.048	0.009	-0.016	-0.003	0.345
Shear force	0.206	0.134	-0.035	0.532	0.090
L*	-0.199	0.569	0.471	-0.054	0.410
a*	-0.324	-0.261	0.005	0.015	-0.579
b*	-0.248	0.0004	0.133	0.251	-0.444

[1] SE of phenotypic correlations ranges from 0.030 to 0.082, SE of genetic correlations ranges from 0.044 to 0.317.