Animal Variation in Lean Color Stability

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Lean color is the primary quality attribute considered by consumers making purchasing decisions. Meat products that do not meet consumer expectations for color are discriminated against and, thus, must be either discounted or discarded, costing the industry as much as $1 billion annually (Smith et al., 2000). Industry sources indicate that some carcasses produce cuts with insufficient color life for case-ready product lines, resulting in significant losses to the industry.

Meat color is largely determined by the redox state and ligand binding of myoglobin located in the muscle (for excellent reviews of myoglobin chemistry, the reader is referred to Mancini and Hunt (2005) and AMSA (2012). In a detailed review of the literature pertaining to the biological basis of lean color stability, Faustman and Cassens (1990) identified oxygen consumption, and lipid oxidation as endogenous characteristics that contribute to discoloration of fresh meat, whereas reducing capacity contributes to the maintenance of fresh meat color. These factors influence the muscle's ability to maintain color via their effects on oxygenation, oxidation, and reduction reactions involving myoglobin (Mancini and Hunt, 2005).

As case-ready packaging systems have become more widely used by the retail segments of the industry, specifications for color-life of meat products have increased. Despite anecdotal evidence from the industry that cuts from some carcasses do not possess sufficient color life to meet specifications for case-ready programs, animal-to-animal variation in lean color stability has received relatively little attention in the scientific literature. Research at the U.S Meat Animal Research Center (USMARC) related to lean color and lean color stability has focused on 1) Characterizing animal-to-animal variation in lean color stability, 2) Identifying sources of variation in lean color and lean color stability, and 3) Developing technology to reduce and/or manage variation in lean color and lean color stability. This paper will provide an overview of our progress in characterizing the relative importance of animal variation to meat processors and retailers and discuss sources of animal variation in lean color stability.

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CHARACTERIZATION OF ANIMAL VARIATION IN LEAN COLOR STABILITY.

Some investigators have concluded that animal effects are of little importance as a source of variation in color stability compared to effects such as muscles within a carcass or storage temperature (Hood, 1980; Renerre and Labas, 1987). Thus, few investigations have addressed animal variation in color stability. Color stability research has mostly focused on differences due to ante- or postmortem management (Ledward, 1985; Lawrence et al., 2004; Seyfert et al., 2007) and across muscles (Talmant et al., 1986; McKenna et al., 2005).

King et al. (2011b) indicated that inter-animal effects contributed to variation in beef lean color stability, though that contribution was smaller than muscle effects within the carcass, particularly early in the display period. Clearly, the gross differences across muscles in the histochemical properties regulating color stability would be expected to be larger than those in homologous muscles across animals. However, the relative contribution of the animal effect to variation in color traits increased as the display period progressed to a point that was equal to muscle effects (King et al., 2011b).

Generally, the variation in color (or discoloration) observed in a given muscle across animals increased as time in display increased (King et al., 2011b). However, in the most color labile muscles, the increase in variation occurred earlier in the display period than in the more color stable muscles, and as these muscles reached maximum discoloration, variation decreased. Thus, the extent of correlation in instrumental color values across muscles changed as the display period progressed. For example the variation in color values of the sirloin cap portion of the biceps femoris (the most labile muscle) increased up to day 3 of display and then decreased, whereas the variation observed in the longissimus lumborum increased throughout the 9 day display period. Consequently, the correlation in color values were maximal when day 3 sirloin cap values were compared to day 9 longissimus

lumborum values. When correlation coefficients were calculated across muscles at the peak in variation in lean color values, all major muscles were moderately to highly correlated to longissimus lumborum color values determined on day 9 of display at some point during display. Thus, strategies to manage variation in longissimus lumborum lean color stability would positively influence other muscles within the carcass. A high degree of correlation across muscles indicated that the influence of animal effects was consistent across muscles.

Hood (1980) and Renerre and Labas (1987) reported variance component estimates that are remarkably consistent with the results of King et al. (2011b). However, despite statistical significance, ($P < 0.01$) of animal effects, both of those investigators concluded that animal variation in color stability was less important in comparison to the influence of muscle effects. However, the evidence indicates that animal effects consistently explain variation in color stability in the hands of multiple investigators which highlights its importance as a factor influencing color stability.

In a study of the seven most prevalent breeds in the U.S. beef herd, King et al. (2010) reported that initial lean color attributes were not heritable. However, in that study, heritability estimates for lean color attributes at the conclusion of display and the change in these variables during display were moderately heritable (h^2 ranged from 0.13 to 0.41), suggesting that significant opportunity exists for reducing premature discoloration through genetic selection. Furthermore, this work provides evidence that genetic factors play a greater role in maintaining lean color than in determining initial color values. Pratt et al. (2013) reported that instrumental redness (a*) and yellowness (b*) values were moderately heritable in beef ($h^2 = 0.29$ and 0.28, respectively). Newcom et al. (2004) reported that initial values for CIE color space values of pork longissimus were moderately to highly heritable (h^2 ranged from 0.52 to 0.98). These studies clearly demonstrate the existence of inherent animal-to-animal differences for lean color and lean color stability in beef and pork, and that lean color could be improved through genetic selection.

King et al. (2010) reported that sire breed had little effect on color of beef longissimus thoracis steaks at the beginning of the display period. However, color at the end of display and change in color during display was affected by sire breed. In general, Charolais and Limousin inheritance resulted in increased color stability compared to the other breeds investigated. Angus, Red Angus, and Hereford inheritance was associated with decreased color stability compared to other breeds included in the experiment. Simmental and Gelbvieh inheritance resulted in intermediate color stability characteristics. Wheeler et al.(2005) reported breed comparisons for carcass and palatability traits of F_1 steer progeny of the population that produced the sires and dams of the animals evaluated by King et al. (2010). Rankings of these breeds with regard to color stability indicating traits are generally consistent with the ranking of these breeds with regard to carcass yield, and inversely related to the rankings of these breeds with regard to marbling score. Perhaps, metabolic differences that contribute to increased muscle and reduced fatness in these breeds are also associated with increased color life.

Faustman and Cassens (1991) reported that beef longissimus and gluteus medius steaks from Holstein steers were more color labile versus those from crossbred beef steers. Those investigators suggested that selection for milk production may have made muscle metabolism in Holstein steers more oxidative than in crossbred steers, resulting in darker and more labile lean color. In support of this premise, Lanari and Cassens (1991) found longissimus and gluteus medius muscles from Holstein carcasses to have greater oxygen consumption rate, metmyoglobin reducing activity, and more labile lean color than muscles from crossbred beef carcasses. King et al. (2010) reported that animals from breeds with the most stable lean color generally had lower myoglobin concentrations than animals from the other breeds.

Genetic differences such as breed type, has been demonstrated to influence muscle metabolism by shifting fiber types. Cuvelier et al. (2006) reported that Angus bulls had greater cytochrome c oxidase activity, lower lactate dehydrogenase activity, and lower L* values than Limousin and Belgian Blue bulls. Vestergaard et al. (2000)reported that an extensive, forage based production system increased the proportion of □-red muscle fibers, pigment concentration, decreased lightness values, and decreased redness values in beef longissimus muscles relative to an intensive, concentrate based production system. Ozawa et al. (2000) reported that Japanese Black steers from multiple closed herds differed with regard to longissimus fiber type distribution and fiber size. Moreover, lean color was positively correlated with □- and □-red muscle fiber diameter. Thus, it is evident, differences in muscle metabolism that are genetically influenced though environmental effects would also play a large role in determining these characteristics. May et al. (1977) reported that Limousin × Angus crossbred steers had a greater proportion of □-white muscle fibers in the longissimus muscle than Hereford × Angus and Simmental × Angus crossbred steers. Johnston et al. (1975) reported that longissimus muscles from Charolais steers had larger fiber areas of all types, and □-white fibers in particular, when compared to longissimus muscles from Angus steers.

BIOCHEMICAL BASIS FOR ANIMAL VARIATION IN LEAN COLOR STABILITY.

Inherent muscle metabolic characteristics such as pigment concentration, mitochondrial oxygen consumption, and reducing capacity through enzymatic and non-enzymatic mechanisms have been implicated in regulating color stability (Faustman and Cassens, 1990; Bekhit and Faustman,

2005; Mancini and Hunt, 2005). It is well understood that these factors differ among muscles within a carcass (Sammel et al., 2002b; McKenna et al., 2005; Seyfert et al., 2006). These characteristics are related to muscle fiber type distributions, which are known to differ considerably across muscles that differ in location and function within the living animal (Hunt and Hedrick, 1977; Klont et al., 1998). Muscles with greater concentration of red fibers have greater concentrations of mitochondria and rely more on oxidative metabolism as a result of having greater concentrations of mitochondria. The enzyme systems responsible for oxygen consumption and metmyoglobin reducing activity are part of the electron transport chain located in the mitochondria (Tang et al., 2005a; Tang et al., 2005b).

Differences in color stability across muscles have generally been attributed to greater oxygen consumption in muscles with less stable color attributes (Faustman and Cassens, 1991; Lanari and Cassens, 1991; McKenna et al., 2005), because oxygen scavenging enzymes compete with myoglobin for oxygen creating oxidative conditions that favor metmyoglobin formation (O'Keeffe and Hood, 1982; Ledward, 1985). Moreover, the cherry-red oxymyoglobin layer is thinner in steaks from muscles with greater oxidative metabolism. Results presented by Ledward (1985) and Cheah and Ledward (1997) suggest that oxygen consumption plays a significant role in metmyoglobin formation initially, but as oxygen consumption decreases with postmortem storage, reducing activity becomes the predominant factor in maintaining stability.

Muscles with increased oxidative metabolism also would have greater metmyoglobin reductase activity (essentially enzyme concentration; Echevarne et al., 1990), because this enzyme is associated with the electron transport chain. However, the role of metmyoglobin reductase activity in maintaining myoglobin in the reduced state has been debated in the literature. Numerous investigators have reported little relationship between metmyoglobin reductase activity and metmyoglobin formation (O'Keeffe and Hood, 1982; Echevarne et al., 1990; Lanari and Cassens, 1991). Others have indicated metmyoglobin reducing activity is important in inhibiting discoloration (Ledward, 1985; Bekhit et al., 2003; Mancini et al., 2008). Echevarne et al. (1990) suggested that NADH, which is required for metmyoglobin reduction via enzymatic and non-enzymatic processes, may be the limiting factor in maintaining myoglobin in the reduced state rather than reductase concentration. In support of this notion, it has been suggested that specific reductase assays with excess NADH effectively differentiate muscles differing in color stability, but not steaks of a common muscle with different levels of discoloration (Sammel et al., 2002a; McKenna et al., 2005).

King et al. (2011a) reported that oxygen consumption measured at the initiation of display was negatively correlated to color stability during simulated retail display, whereas all of the measures of metmyoglobin reducing ability determined on day 0 or 6 of display were positively correlated to color stability. Correlations between reducing activity and color stability data were slightly stronger on d 6 than they were on d 0. Furthermore, steaks with stable lean color retained a greater proportion of their ability to reduce nitric oxide metmyoglobin after 6 d of display than those with more labile lean color. Thus, it appears that initial levels of reducing capacity are important in determining color stability, but variation in the ability to maintain or regenerate reducing ability is also important in regulating color stability. The stronger relationships between reducing ability and color stability detected at the end of display may be due to variation in the muscle's ability to replenish the NADH pool needed to facilitate continued reduction.

The mechanism for this effect appears to be the regeneration of NADH by metabolic enzymes that remain active in postmortem muscle (Kim et al., 2006; Kim et al., 2009b; Mohan et al., 2010a). Studies have indicated that including metabolic intermediates in marination formulations has increased color life (Kim et al., 2006; Kim et al., 2009a; Mohan et al., 2010b). However, this phenomenon has not been demonstrated to occur in normal postmortem muscle with endogenous levels of these metabolites.

Sammel et al. (2002a) suggested that very low oxygen consumption levels were deleterious to color stability because mitochondrial respiration was needed to regenerate NADH to be used as a cofactor in metmyoglobin reduction. If this is true, oxygen consumption and metmyoglobin reducing ability would be correlated to some extent. In King et al. (King et al., 2011a), very few relationships were detected between oxygen consumption and measures of reducing activity. In fact, longissimus thoracis steaks classified as having stable lean color had both lower oxygen consumption and greater reducing activity than those with less stable lean color in that study. Using data collected on 19 beef muscles, McKenna et al. (2005) noted that some muscles with similar oxygen consumption levels had very different capacities for metmyoglobin reduction. Those investigators surmised that relationships between oxygen consumption, reducing ability, and color stability are dependent on the relative levels of oxygen consumption and reducing activity i.e. more stable muscle have sufficient reducing ability to mitigate oxygen consumption effects. This may be because some muscles lack the substrates necessary to replenish the NADH necessary for the enzymes to be active. These reports suggest that variation in metmyoglobin reducing ability within a muscle is not simply a function of mitochondrial enzyme concentration, and also is influenced by the metabolic efficiency of the muscle.

The function of mitochondria in postmortem muscle is critical to maintaining lean color stability. Site specific defects have been identified in complex I and complex III of the electron transport chain (Iqbal et al., 2001; Bottje et al., 2002a).

These defects result in electron loss during electron transport, which are a source of reactive oxygen species in muscle. Researchers have shown a link between mitochondrial function, respiratory chain activity and electron leak to feed efficiency in broilers (Bottje et al., 2002b) and cattle (Kolath et al., 2006).

Reactive oxygen species released by these defects could potentially reduce color stability via multiple possible mechanisms. The release of reactive oxygen species into the cell would have an oxidizing effect on proteins within the cell, including myoglobin. Moreover, the reactive oxygen species must then be reduced by the cell, which would deplete reducing equivalents that could be alternatively used to reduce myoglobin. Another possible mechanism is the inhibition of the reducing apparatus, either by making reductase non-functional, or by preventing the regeneration of cofactors needed for myoglobin reduction.

McKeith et al. (2014) incubated isolated mitochondria from beef longissimus from carcasses exhibiting normal lean color and measured electron loss during incubation with glutamate and succinate as substrates. Increased electron loss was associated with decreased nitric oxide metmyoglobin reducing ability (r = -0.23), increased oxidation of sarcoplasmic proteins (r = 0.32), and increased color change as simulated retail display progressed (r = 0.35). Interestingly, increased electron loss by the mitochondria was associated with increased glycolytic potential (r = 0.24). Perhaps muscles with inefficient mitochondrial metabolism compensated by increasing their capacity for energy production through glycolytic means. Our laboratory also has found longissimus muscles from carcasses exhibiting the dark cutting condition to have greater mitochondrial abundance and greater electron loss by mitochondria compared to cohorts from the same production lots exhibiting normal lean color (McKeith, 2014). These results suggest that mitochondrial function is important to lean color and the maintenance of lean color in beef longissimus.

The breed comparisons of King et al. (2010) suggested that color stability was greater in steaks from animals favoring glycolytic metabolism. Although the enzyme systems responsible for myoglobin reduction are located in the mitochondria, mitochondrial abundance is not the primary driver of color stability. McKeith et al. (2014) reported that mitochondrial abundance was associated with lower a* and b* values in beef longissimus steaks at the initiation of simulated retail display, but was not associated with differences in color at the end of display. Canto et al. (2014) subsampled the samples evaluated by McKeith et al. (2014) and compared the proteome of beef longissimus lumborum steaks divergent in lean color stability. Those investigators found three glycolytic enzymes (phosphoglucomutase-1, glyceraldehyde-3-phosphate dehydrogenase, and pyruvate kinase M2) that were over-abundant in color-stable steaks and positively correlated to measures of redness at the conclusion of simulated retail display. These enzymes are directly involved in ATP production during metabolism.

CONCLUSIONS

The biochemical factors affecting lean color stability vary greatly among animals, and are, to some extent, genetically regulated. Genetic effects on lean color stability appear to be mediated through fiber type distributions with animals favoring glycolytic metabolism having greater lean color stability. Moreover, although the enzyme systems responsible for oxygen consumption and metmyoglobin reducing activity are located in the mitochondria, mitochondrial abundance does not appear to be a large determinant of lean color stability. The mitochondria with decreased efficiency are associated with meat with diminished color-life. Moreover, muscles with greater capacity for glycolytic metabolism are associated with increased color-life, presumably from greater stores of NADH or greater ability to regenerate NADH to fuel metmyoglobin reduction.

REFERENCES

AMSA 2012. Meat color measurement guidelines. Hunt, M. C. & King, D. A. (eds.). Champaign, IL: American Meat Science Association.

Bekhit, A.E.D.; Geesink, G.H.; Ilian, M.A.; Morton, J.D.; Bickerstaffe, R. 2003. The effects of natural antioxidants on oxidative processes and metmyoglobin reducing activity in beef patties. Food Chem., 81, 175-187.

Bekhit, A.E.D.; Faustman, C. 2005. Metmyoglobin reducing activity. Meat Sci., 71, 407-439.

Bottje, W.; Iqbal, M.; Tang, Z.; Cawthon, D.; Okimoto, R.; Wing, T.; Cooper, M. 2002a. Association of mitochondrial function with feed efficiency within a single genetic line of male broilers. Poultry Sci., 81, 546-555.

Bottje, W.; Iqbal, Z.X.T.M.; Cawthon, D.; Okimoto, R.; Wing, T.; Cooper, M. 2002b. Association of mitochondrial function with feed efficiency within a single genetic line of broiler. Poultry Sci., 81, 546-555.

Canto, A.C.V.S.; Suman, S.P.; Nair, M.N.; Li, S.; Rentfrow, G.; Beach, C.M.; Silva, T.J.P.; Wheeler, T.L.; Shackelford, S.D.; Grayson, A.L.; McKeith, R.O.; King, D.A. 2014. Differential abundance of sarcoplasmic proteome explains animal effect on beef longissimus lumborum color stability. Meat Sci., in preparation.

Cheah, P.B.; Ledward, D.A. 1997. Inhibition of metmyoglobin formation in fresh beef by pressure treatment. Meat Sci., 45, 411-418.

Cuvelier, C.; Clinquart, A.; Hocquette, J.F.; Cabaraux, J.F.; Dufrasne, I.; Istasse, L.; Hornick, J.L. 2006. Comparison of composition and quality traits of meat from young finishing bulls from belgian blue, limousin and aberdeen angus breeds. Meat Sci., 74, 522-531.

Echevarne, C.; Renerre, M.; Labas, R. 1990. Metmyoglobin reductase activity in bovine muscles. Meat Sci., 27, 161-172.

Faustman, C.; Cassens, R.G. 1990. The biochemical basis for discoloration in fresh meat: A review. J. Musc. Foods, 1, 217-243.

Faustman, C.; Cassens, R.G. 1991. The effect of cattle breed and muscle type on discoloration and various biochemical parameters in fresh beef. J. Anim. Sci., 69, 184-93.

Hood, D.E. 1980. Factors affecting the rate of metmyoglobin accumulation in pre-packaged beef. Meat Sci., 4, 247-265.

Hunt, M.C.; Hedrick, H.B. 1977. Profile of fiber types and related properties of five bovine muscles. J. Food Sci., 42, 513-517.

Iqbal, M.; Cawthon, D.; Wideman Jr, R.F.; Bottje, W.G. 2001. Lung mitochondrial dysfunction in pulmonary hypertension syndrome. I. Site-specific defects in the electron transport chain. Poultry Sci., 80, 485-495.

Johnston, D.M.; Stewart, D.F.; Moody, W.G.; Boling, J.; Kemp, J.D. 1975. Effect of breed and time on feed on the size and distribution of beef muscle fiber types. J. Anim. Sci., 40, 613-620.

Kim, Y.H.; Hunt, M.C.; Mancini, R.A.; Seyfert, M.; Loughin, T.M.; Kropf, D.H.; Smith, J.S. 2006. Mechanism for lactate-color stabilization in injection-enhanced beef. J. Agric. Food Chem., 54, 7856-7862.

Kim, Y.H.; Keeton, J.T.; Smith, S.B.; Berghman, L.R.; Savell, J.W. 2009a. Role of lactate dehydrogenase in metmyoglobin reduction and color stability of different bovine muscles. Meat Sci.

Kim, Y.H.; Keeton, J.T.; Yang, H.S.; Smith, S.B.; Sawyer, J.E.; Savell, J.W. 2009b. Color stability and biochemical characteristics of bovine muscles when enhanced with l- or d-potassium lactate in high-oxygen modified atmospheres. Meat Sci., 82, 234-240.

King, D.A.; Shackelford, S.D.; Kuehn, L.A.; Kemp, C.M.; Rodriguez, A.B.; Thallman, R.M.; Wheeler, T.L. 2010. Contribution of genetic influences to animal-to-animal variation in myoglobin content and beef lean color stability. J. Anim. Sci., 88, 1160-1167.

King, D.A.; Shackelford, S.D.; Rodriguez, A.B.; Wheeler, T.L. 2011a. Effect of time of measurement on the relationship between metmyoglobin reducing activity and oxygen consumption to instrumental measures of beef longissimus color stability. Meat Sci., 87, 26-32.

King, D.A.; Shackelford, S.D.; Wheeler, T.L. 2011b. Relative contributions of animal and muscle effects to variation in beef lean color stability. J. Anim Sci., 89, 1434-1451.

Klont, R.E.; Brocks, L.; Eikelenboom, G. 1998. Muscle fibre type and meat quality. Meat Sci., 49, Supplement 1, S219-S229.

Kolath, W.H.; Kerley, M.S.; Golden, J.W.; Shahid, S.A.; Johnson, G.S. 2006. The relationships among mitochondrial function and residual feed intake in steers. J. Anim. Sci., 84, 861-865.

Lanari, M.C.; Cassens, R.G. 1991. Mitochondrial activity and beef muscle color stability. J. Food Sci., 56, 1476-1479.

Lawrence, T.E.; Dikeman, M.E.; Hunt, M.C.; Kastner, C.L.; Johnson, D.E. 2004. Effects of enhancing beef longissimus with phosphate plus salt, or calcium lactate plus non-phosphate water binders plus rosemary extract. Meat Sci., 67, 129-137.

Ledward, D.A. 1985. Post-slaughter influences on the formation of metyyoglobin in beef muscles. Meat Sci., 15, 149-171.

Mancini, R.A.; Hunt, M.C. 2005. Current research in meat color: 51st international congress of meat science and technology (icomst). Meat Sci., 71, 100-121.

Mancini, R.A.; Seyfert, M.; Hunt, M.C. 2008. Effects of data expression, sample location, and oxygen partial pressure on initial nitric oxide metmyoglobin formation and metmyoglobin-reducing-activity measurement in beef muscle. Meat Sci., 79, 244-251.

May, M.L.; Dikeman, M.E.; Schalles, R. 1977. Longissimus muscle histological characteristics of simmental × angus, hereford × angus and limousin × angus crossbred steers as related to carcass composition and meat palatability traits. J. Anim. Sci., 44, 571-580.

McKeith, R.O. 2014. The biological basis for animal variation in lean color stability. Master's Thesis, Texas A&M University, College Station, TX

McKeith, R.O.; King, D.A.; Grayson, A.L.; Shackelford, S.D.; Savell, J.W.; Wheeler, T.L. 2014. Influence of mitochondrial efficiency on beef lean color stability. Meat Sci., 96, 476.

McKenna, D.R.; Mies, P.D.; Baird, B.E.; Pfeiffer, K.D.; Ellebracht, J.W.; Savell, J.W. 2005. Biochemical and physical factors affecting discoloration characteristics of 19 bovine muscles. Meat Sci., 70, 665-682.

Mohan, A.; Hunt, M.C.; Barstow, T.J.; Houser, T.A.; Muthukrishnan, S. 2010a. Effects of malate, lactate, and pyruvate on myoglobin redox stability in homogenates of three bovine muscles. Meat Sci., 86, 304-310.

Mohan, A.; Hunt, M.C.; Muthukrishnan, S.; Barstow, T.J.; Houser, T.A. 2010b. Myoglobin redox form stabilization by compartmentalized lactate and malate dehydrogenases. J. Agric. Food Chem., 58, 7021-7029.

Newcom, D.W.; Stalder, K.J.; Baas, T.J.; Goodwin, R.N.; Parrish, F.C.; Wiegand, B.R. 2004. Breed differences and genetic parameters of myoglobin concentration in porcine longissimus muscle. J. Anim. Sci., 82, 2264-8.

O'Keeffe, M.; Hood, D.E. 1982. Biochemical factors influencing metmyoglobin formation on beef from muscles of differing colour stability. Meat Sci., 7, 209-228.

Ozawa, S.; Mitsuhashi, T.; Mitsumoto, M.; Matsumoto, S.; Itoh, N.; Itagaki, K.; Kohno, Y.; Dohgo, T. 2000. The characteristics of muscle fiber types of longissimus thoracis muscle and their influences on the quantity and quality of meat from japanese black steers. Meat Sci., 54, 65-70.

Pratt, P.J.; Moser, D.W.; Thompson, L.D.; Jackson, S.P.; Johnson, B.J.; Garmyn, A.J.; Miller, M.F. 2013. The heritabilities, phenotypic correlations, and genetic correlations of lean color and palatability measures from longissimus muscle in beef cattle. J. Anim. Sci., 91, 2931-2937.

Renerre, M.; Labas, R. 1987. Biochemical factors influencing metmyoglobin formation in beef muscles. Meat Sci., 19, 151-165.

Sammel, L.M.; Hunt, M.C.; Kropf, D.H.; Hachmeister, K.A.; Johnson, D.E. 2002a. Comparison of assays for metmyoglobin reducing ability in beef inside and outside semimembranosus muscle. J. Food Sci., 67, 978-984.

Sammel, L.M.; Hunt, M.C.; Kropf, D.H.; Hachmeister, K.A.; Kastner, C.L.; Johnson, D.E. 2002b. Influence of chemical characteristics of beef inside and outside semimembranosus on color traits. J. Food Sci., 67, 1323-1330.

Seyfert, M.; Mancini, R.A.; Hunt, M.C.; Tang, J.; Faustman, C.; Garcia, M. 2006. Color stability, reducing activity, and cytochrome c oxidase activity of five bovine muscles. J. Agric. Food Chem., 54, 8919-25.

Seyfert, M.; Mancini, R.A.; Hunt, M.C.; Tang, J.; Faustman, C. 2007. Influence of carbon monoxide in package atmospheres containing oxygen on colour, reducing activity, and oxygen consumption of five bovine muscles. Meat Sci., 75, 432-442.

Smith, G.C.; E, B.K.; Sofos, J.N.; Tatum, J.D.; Williams, S.N. 2000. Economic implications of improved color stability in beef. In: Decker, E. A., Faustman, C. & Lopez-Bote, C. J. (eds.) Antioxidants in muscle foods: Nutritional strategies to improve quality New York: Wiley-Interscience.

Talmant, A.; Monin, G.; Briand, M.; Dadet, M.; Briand, Y. 1986. Activities of metabolic and contractile enzymes in 18 bovine muscles. Meat Sci., 18, 23-40.

Tang, J.; Faustman, C.; Hoagland, T.A.; Mancini, R.A.; Seyfert, M.; Hunt, M.C. 2005a. Postmortem oxygen consumption by mitochondria and its effects on myoglobin form and stability. J. Agric. Food Chem., 53, 1223-30.

Tang, J.; Faustman, C.; Mancini, R.A.; Seyfert, M.; Hunt, M.C. 2005b. Mitochondrial reduction of metmyoglobin: Dependence on the electron transport chain. J. Agric. Food Chem., 53, 5449-55.

Vestergaard, M.; Oksbjerg, N.; Henckel, P. 2000. Influence of feeding intensity, grazing and finishing feeding on muscle fibre characteristics and meat colour of semitendinosus, longissimus dorsi and supraspinatus muscles of young bulls. Meat Sci., 54, 177-185.

Wheeler, T.L.; Cundiff, L.V.; Shackelford, S.D.; Koohmaraie, M. 2005. Characterization of biological types of cattle (cycle vii): Carcass, yield, and longissimus palatability traits. J. Anim. Sci., 83, 196-207.