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Exogenous and Endogenous Factors Influencing Color of Fresh Meat from Ungulates

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Abstract: Biochemistry of post-mortem muscle tissue is complex, and several factors affect the fresh meat color and color stability, both of which influence consumer acceptance. Therefore, improving meat color and meat color stability is of significant value to the meat industry and consumers. While extensive literature is available on the color and color stability of domestic ungulates, literature on wild ungulates is notably lacking. With an increasing global demand for meats from wild ungulates, it is critical to identify the knowledge gaps regarding their color and color stability. The objective of this paper is to overview the exogenous and endogenous factors influencing the color and color stability of fresh meats from domestic and wild ungulates. The literature highlighted that the pre- and post-harvest factors influencing meat color and meat color stability are interrelated and not mutually exclusive. Current research indicates that the effects of several of these factors are specific to species, breed, and muscle source. Novel ways to manipulate these factors using a biosystems approach should be explored to improve color attributes of fresh ungulate meats.

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Introduction

The criticality of fresh meat color to consumer acceptance and purchasing intent has been extensively documented (Faustman and Cassens, 1990; Risvik, 1994; Mancini and Hunt, 2005; Hoffman et al., 2007; Faustman et al., 2010; Suman and Joseph, 2013; Suman et al., 2014). In red meats, a bright cherry-red color is preferred by consumers, whereas brown discoloration is not acceptable (Mancini and Hunt, 2005; Suman et al., 2014). Consumers perceive bright cherry-red meat as being more fresh and wholesome in comparison to discolored meat (Kropf, 1980; Faustman and Cassens, 1990; Mancini and Hunt, 2005; Suman et al., 2014). Although meat discoloration may be indicative of quality, it may not be always be the case (Morrissey et al., 2008). Nonetheless, consumers still use color as their best indicator for wholesomeness as it is the only trait they can evaluate at the point of sale (Mancini and Hunt, 2005; Suman et al., 2014).

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In the global market, where the demand for meat from exotic species is increasing (Hoffman and Cawthorn, 2013), fresh meat from wild ungulates, such as deer and various game species, has considerable market potential (Hoffman and Wiklund, 2006). While extensive research has been done on the color of fresh red meats harvested from various conventional livestock, information on venison and game meat color is limited, if not nonexistent. Thus, the quality aspects of meat from wild ungulates need to be examined thoroughly to establish baseline for these species.

Mancini and Hunt (2005) overviewed the applied aspects of color and color stability in beef and pork, while other reviews focused on the biochemistry of color in red meats and poultry (Suman and Joseph, 2013) and practical strategies for improving beef color (Suman et al., 2014). The aim of this review is to identify potential areas for further research in the color and color stability of meat from both domestic and wild ungulates, with emphasis on research and development in the past 2 decades, to advance the knowledge on fresh meat color.

For the purposes of this review, game meat refers to meat from game animals in Africa, whereas venison refers to meat from deer species originating elsewhere. The reason for this distinction is that meat from game animals in Africa generally originates from wild, free roaming animals, whereas venison is increasingly being used to refer to farmed/domesticated deer species (Hoffman and Wiklund, 2006).

Meat Color and Myoglobin Chemistry

Meat obtained from ungulates is red in color, which primarily is due to the presence of the myoglobin (Mb) in skeletal muscles (Giddings, 1977; Livingston and Brown, 1981). Other heme proteins (hemoglobin and cytochromes) may also contribute to the color of red meat, but to a far lesser extent (Faustman and Suman, 2017; Suman and Joseph, 2014). The color of fresh meat is influenced by the amount and chemical state of Mb (Faustman and Cassens, 1990; Mancini and Hunt, 2005; Suman and Joseph, 2013; Suman and Joseph, 2014) and by the structure of the muscle tissue, which is directly related to its ultimate pH (Insausti et al., 1999).

Myoglobin structure and function

Mb is a protein and, as with all proteins, it is susceptible to changes in response to the external environmental conditions. Changes in pH or temperature could cause protein denaturation, which can alter the structure and functionality of the protein (Solomon et al., 1998). These changes could have a dramatic effect on the color of the meat (Kim et al., 2014).

Mammalian Mb is an intracellular, iron containing, monomeric globular heme protein consisting of 153 amino acids (Renerre, 2000) found in cardiac and skeletal muscles (Livingston and Brown, 1981). It is water-soluble and consists of eight right-handed α helices (designated A to H) with a central hydrophobic core. Inside the hydrophobic core is a prosthetic heme group consisting of a porphyrin ring with a central iron atom. The iron has 6 available valence electrons; four of which are bound to the porphyrin ring via the nitrogens of the pyrroles, one of which is bound to an imidazole ring from the proximal histidine (histidine residue at position 93) on the globin protein, and one which is available to bind reversibly to various ligands. A distal histidine (position 64) is also present in the vicinity of the porphyrin ring, and although it is not bound to the iron, it may influence the dynamics of ligand binding to the sixth position of the heme iron (Livingston and Brown, 1981).

Myoglobin binds reversibly with oxygen, serves as oxygen storage protein, and can enhance oxygen availability, particularly when oxygen partial pressure is low (Bailey et al., 1990). In the living muscle cells, Mb facilitates the diffusion of oxygen from the extracellular space to the mitochondria (Wittenberg and Wittenberg, 1989). Myoglobin thus supplies the oxygen necessary for various biological processes (Wittenberg and Wittenberg, 2003) and is the protein responsible for transporting oxygen within the living muscles (Livingston et al., 1983; Renerre, 2000). This oxygen is intimately involved in the oxygen consumption activity of meat (Mancini and Hunt, 2005).

Myoglobin redox forms in fresh meat

Formation of Mb redox forms depends on the specific ligand bound to the heme iron and to the redox state of the iron, which is either reduced (Fe^{2+}) or oxidized (Fe^{3+}). Oxygen is a ligand bound only to Fe^{2+}. The predisposition of the iron in Mb to bind to oxygen causes it to oxygenate readily post-mortem, resulting in blooming. The 3 major redox forms of Mb in fresh meat are deoxymyoglobin (DeoxyMb), oxymyoglobin (OxyMb) and metmyoglobin (MetMb). Other ligands, carbon monoxide and nitric oxide, have been discussed elsewhere (Mancini and Hunt, 2005; Suman and Joseph, 2013).

Deoxymyoglobin is the redox state of Mb where no ligand is bound to the sixth binding site on the iron and the iron is in its reduced state (Fe^{2+}). This

state can only be maintained under anoxic conditions, where very low oxygen tension occurs such as vacuum packaging and the interior of post-mortem muscle. Thus it is indicative of freshly cut meat prior to blooming or meat which is vacuum-packaged, and in this redox state meat is perceived as purple/purplish-red. The consumer perception to the purple/purplish-red color of DeoxyMb is low, and therefore, displaying meat in vacuum packaging may negatively influence sales (Carpenter et al., 2001).

When DeoxyMb is exposed to oxygen, a bright cherry-red OxyMb is formed through oxygenation, and this process is known as blooming in industry. In this state, diatomic oxygen is bound to the sixth binding site of the iron, which remains in the reduced state (Fe^{2+}). This binding also makes OxyMb less liable to oxidation than DeoxyMb. As the exposure to oxygen increases, the depth of the oxygen penetration in meat increases and therewith the thickness of the OxyMb layer. The thickness of this layer is highly dependent on various factors; thickness decreases as the pH and meat temperature increase, and the layer thickens with the increases in the oxygen partial pressure and oxygen exposure time and reduced competition from respiratory enzymes (Suman and Nair, 2017). With the increase in the thickness of this OxyMb layer, there is a concurrent increase in saturation of the bright cherry-red color, which the consumers find more aesthetically desirable (Stevenson et al., 1989; Young and West, 2001; Mancini and Hunt, 2005; Suman et al., 2014).

The oxidation of OxyMb as well as DeoxyMb to MetMb causes the change in color of meat surface to brown. In MetMb, the heme iron is in an oxidized ferric (Fe^{3+}) state, and the ligand binding site of heme iron is occupied by water (Faustman and Suman, 2017). Consumers find the brown color of MetMb undesirable and indicative of poor quality or spoilage (Kropf, 1980; Faustman and Cassens, 1990; Rosenvold and Andersen, 2003a; Mancini and Hunt, 2005). When concentrations of MetMb approach 20% on the surface of meat, consumer acceptance and sales decline (Warriss, 2000). In meat with a normal pH, MetMb forms spontaneously from DeoxyMb when minute amounts of oxygen (0.5 to 3%) leak into vacuum packaged meat and from OxyMb when the oxygen partial pressure is reduced to 0.5 to 3% by the native oxygen consumption metabolism of meat (Brooks, 1938). Other conditions favoring MetMb formation are warmer temperatures, impairment of reducing conditions, and elevated microbial growth that may occlude oxygen exposure of meat (Faustman and Cassens, 1990).

Factors Influencing Meat Color

The color of meat can be evaluated visually and instrumentally (American Meat Science Association, 2012). While visual evaluation is subjective in nature and is done by panelists (American Meat Science Association, 2012), instrumental evaluation is objective and is accomplished by reflectance spectrophotometry (Krzywicki, 1979). A variety of colorimeters and spectrophotometers are employed for instrumental evaluation, which gives physical description of the color, such as the L^* (lightness), a^* (redness), and b^* (yellowness), chroma (saturation index), and hue angle values (American Meat Science Association, 2012). Furthermore, spectrophotometry can estimate the relative proportions of various Mb redox forms on meat surface using specific wavelengths unique to each redox state (Krzywicki, 1979). Both instrumental and visual evaluations correspond well to consumer perception of meat color (American Meat Science Association, 2012).

Meat comes from living animals, and the skeletal muscles are adapted to the environment in which the animal resides and their need to respond to various stimuli (Warner et al., 2010; England et al., 2013). Numerous exogenous and endogenous factors affect fresh meat color. The complexity of the interactions between these factors makes understanding and control of meat color very challenging.

Extrinsic factors

Season

Seasonal variations in physical and chemical aspects of meat quality have been documented (Kim et al., 2003; Węglarz, 2010; Wiklund et al., 2010; Neethling et al., 2014). The seasonal differences in meat color can be attributed to differences in physical activity, stress, and/or differences in diet between seasons, which result in differences in the muscle composition (Neethling et al., 2014) and pH (Wiklund et al., 2010).

In Hanwoo (Korean native) cattle, the L^* values (lightness) were the lowest during winter and the highest in autumn and spring, a^* (redness) and chroma values were the highest for spring and summer and the lowest in winter, and b^* values (yellowness) were the highest in summer and autumn and the lowest in winter, and hue angle values were the highest in summer and the lowest in winter (Kim et al., 2003). Contradictory to these results, Węglarz (2010) found that the cattle slaughtered in winter generally had greater L^*, a^*, b^*,

hue angle and chroma values than those slaughtered in summer. Similar results were reported by Kadim et al. (2004a) for the *L**, *a**, and *b** values of cattle in a study examining meat color differences between summer and winter. These disagreements between the aforementioned investigations may be attributed to differences in geographical locations of the studies and breed of the cattle used.

Differences in the color stability of red deer (*Cervus elaphus*) Longissimus thoracis et lumborum varied between seasons, with venison from deer harvested in summer having the poorest color stability and in spring the best. The venison from animals harvested during summer and spring had low (pH 5.46) and high (pH 5.62) values, respectively (Wiklund et al., 2010). Low pH values are known to result in poor meat color stability, whereas high pH values lead to improved color stability (Livingston and Brown, 1981). In addition, the superior quality pasture in spring, which leads to higher levels of antioxidants in the muscle, also contributed to the improved color stability of spring-harvested animals (Wiklund et al., 2006).

Increased incidences of dark, firm and dry (DFD) beef carcasses were reported for cattle slaughtered during the summer (Kreikemeier et al., 1998; Mitlöhner et al., 2002; Kadim et al., 2004a). These cattle seemed more prone to physiological (heat) stress and had lower glycogen reserves than animals slaughtered during winter (Kadim et al., 2004a). In contrast, Miranda-de la Lama et al. (2009) observed greater incidences of DFD in lamb meat during winter, and these findings support similar observations by Knowles et al. (1998) and Zahner et al. (2004), who reported elevated stress levels in lambs and dairy cows during winter, respectively.

Seasonal effects on meat color may be related to differences in animal behavior (e.g., mating vs. non-mating season), quality of the pasture, and susceptibility to physiological stress. Discrepancies in observations also exist, and it seems that seasonal effects may be confounded by other factors such as geographical location and species/breed of the animals. Limited scientific literature is available on the effects of season on the color stability of game species. Although hunting of game species is generally restricted to winter season (typically after the breeding and rutting seasons), certain species, such as the springbok (*Antidorcas marsupialis*), are hunted throughout the year (Hoffman and Wiklund, 2006). Additional research is required to elucidate the effects of season on the meat color stability of game species, particularly those hunted year-round.

Feeding management

Priolo et al. (2001) compiled a review on the effects of pasture and concentrate feeding on meat color and flavor in ruminants. Meat from animals finished on pasture diets was darker (lower *L** values) than meat from animals finished on concentrate diets. Several factors were responsible for the observed difference, with the pH and intramuscular fat appearing to have the largest influence.

Color and color stability can be affected by the feeding management involving extensive (grass/pasture/forage) or intensive (concentrate/grain/feedlot) systems. Feeding strategy resulting in high levels of antioxidants (e.g., vitamin E) in muscles could lead to improved color stability. Supplementation of vitamin E counteracts lipid oxidation and consequently improves the color stability of meat (Lynch et al., 1998, 1999) . The effect of vitamin E on color stability was species-specific, with the antioxidant improving color stability in beef (Faustman et al., 1989; Arnold et al., 1992) and lamb (Strohecker et al., 1997), but not in pork (Cannon et al., 1996; Houben et al., 1998; Phillips et al., 2001). In addition, diet can influence the concentration of rumen volatile fatty acids, which could influence the glycogen deposition in the muscle and subsequently the pH and color of the meat (Daly et al., 1999; Priolo et al., 2001).

The pH is very important in meat color and is one of the major reasons for the differences reported between pasture- and grain-based systems. Pasture-raised beef animals may have an insufficient energy intake leading to elevated meat pH (Daly et al., 1999). The higher pH in pasture-raised animals could also be attributed to the differences associated with the production systems. Beef cattle reared on extensive pasture systems have minimal human contact and handling in comparison to feedlot animals. Thus, pasture-raised animals could be more susceptible to pre-slaughter stress, which in turn could lead to a decrease in pre-slaughter muscle glycogen content and high pH in the meat (Daly et al., 1999). Furthermore, feeding systems can also influence fat color particularly the subcutaneous fat, with pasture-based diets resulting in prominent yellow fat compared to grain-based diets. The increase in yellowness is due to an increased deposition of carotene (from green leaves) in the fat of ruminants (Yang et al., 1992). Most game species do not have thick layers of subcutaneous fat; however, female game animals that do not conceive within a given year/season had thick layers of subcutaneous fat (Hoffman and Wiklund, 2006).

Díaz et al. (2002) found no differences in the color for the rectus abdominis, but observed lower *L** values in the longissimus muscle from lambs on pasture than in the longissimus from concentrate-fed lambs. The darker

meat color of the pasture lambs was attributed to higher Mb concentrations due to higher physical activity than their concentrate-fed counterparts (Vestergaard et al., 2000). Differences in subcutaneous fat color were also observed (Díaz et al., 2002), with the pasture lambs having darker (lower *L** value) and yellower (higher *b** value) fat. Luciano et al. (2012) observed no differences for the initial bloomed meat color of pasture versus concentrate-fed lambs; however, the color stability of meat from pasture-raised lambs was greater than that from concentrate-fed lambs. The differences in color stability were attributed to the high concentration of antioxidants (from the greens) in the muscle tissue of pasture lambs (Wood and Enser, 1997; Faustman et al., 2010). Interestingly, the time on pasture (4 h daily vs. 8 h daily) did not have an effect on the color stability (Luciano et al., 2012).

Differences in meat and subcutaneous fat color have been observed for beef fed on concentrate and forage diets. In agreement with Priolo et al. (2001), Avilés et al. (2015) documented that forage-based diets led to darker (lower *L** values) beef in comparison to concentrate-based diets. While the meat *a** (redness) value was not affected by the feeding system, the *b** values (yellowness) were impacted, with concentrate-diets resulting in lower *b** values in comparison to forage diets. These results were congruent with those of Daza et al. (2014). Several other studies also have noted higher *b** values (more yellowness) for subcutaneous fat of cattle raised on forage (Cooke et al., 2004; Duckett et al., 2013; Avilés et al., 2015). The increase in yellowness is attributed to the high carotenoid content in forage-based diet (Casasus et al., 2012).

Vestergaard et al. (2000) investigated the influence of feeding system (pasture vs. concentrates) on muscle fiber type and the consequential effects of muscle fiber type on color. The effect of the production system on muscle fiber type was mainly attributed to differences in physical activity and feeding level and to a lesser extent the diet (pasture vs. concentrates). Overall, an extensive rearing system led to higher levels of physical activity in comparison to intensive rearing, which resulted in meat from extensively reared animals having more slow-contracting fibers, higher oxidative metabolic potential and a darker appearance than their intensively-raised counterparts.

Venison from animals fed diets that increased the concentration of antioxidants in the meat had improved color stability (Wiklund et al., 2006, 2010). Similar findings were reported for lamb (Díaz et al., 2002; Perlo et al., 2008) and beef (Lanari et al., 2002). Wiklund et al. (2006) found that deer meat from animals fed pellets had a lower pH and greater *a** values than the meat from grazing animals. The lower pH results in lower mitochondrial activity and lower oxygen consumption (Tang et al., 2005), which subsequently lead to rapid Mb oxygenation, increased blooming, and deeper penetration of the cherry-red OxyMb layer (Ramanathan et al., 2013).

Grazing generally results in higher levels of polyunsaturated fatty acids (PUFA; Wood et al., 2004), which are prone to oxidation (Morrissey et al., 1998). A positive correlation between Mb stability and lipid oxidation has been explained (Faustman et al., 2010), and thus increased lipid oxidation leads to increased Mb oxidation and discoloration (Yin and Faustman, 1993). However, beef from grazing animals also generally contains higher concentrations of antioxidants, which can protect against lipid and myoglobin oxidation (Insani et al., 2008). Wiklund et al. (2006) found that the venison from grazing animals had better color stability than meat from pellet-fed animals, possibly due to higher levels of vitamin E. In contrast, other studies on venison reported no differences in meat color between concentrate and pasture diets (Volpelli et al., 2003; Hutchison et al., 2012). Although Gatellier et al. (2005) have implicated color and color stability variations on differences in Mb content in animals fed different diets, Wiklund et al. (2006) observed no differences in Mb content between meat from pellet-fed and grazing animals.

In Africa, game species are reared only in extensive production systems, although some species are known to inhabit small territories (Hoffman et al., 2008). Nonetheless, scientific literature on antioxidant levels in game meat and the effect of feeding systems on the meat color and color stability of game species is nonexistent.

Ante-mortem stress

Ante-mortem stress has two sub-categories: acute and prolonged ante-mortem stress. Acute ante-mortem stress is typically associated with meat characterized as pale, soft, and exudative (PSE), whereas prolonged ante-mortem stress results in meat that is dark cutting, which is also known as dark, firm, and dry (DFD). This terminology can be applied to any species, and over the years other variations in meat color quality have been reported and are detailed below.

Acute, short-term (from minutes to a few hours) ante-mortem stress can lead to PSE meat that forms when the post-harvest carcass pH declines more rapidly than normal while the carcass temperature is relatively high. This combination of undesirable conditions increases protein (both myofibrillar and sarcoplasmic) denaturation, which decreases water holding capacity (WHC) and results in a shift of intracellular water and Mb into interfibrillar spaces (Warriss, 2000). Thus, muscle struc-

ture becomes softer and more "open", which increases the light scattering and a more pale visual appearance (Warriss, 2000; Lawrie and Ledward, 2006).

Various studies have investigated the occurrence of PSE in pork (Aalhus et al., 1998; Bendall and Wismer-Pedersen, 1962; Bowker et al., 2000; Briskey, 1964; Guàrdia et al., 2005; Lewis et al., 1987; O'Neill et al., 2003; Rosenvold and Andersen, 2003a, 2003b). The PSE condition occurs most commonly in porcine muscle with either the halothane (Haln) or Rendement Napole (RN-) genes, but it has been reported in pigs without these genes (Rosenvold and Andersen, 2003a). The PSE meat also has been observed in beef (Aalhus et al., 1998; Hunt and Hedrick, 1977a,b; Warriss, 2000) and in other ungulates (Hoffman, 2001a). Additionally, Hoffman (2001a) reported incidences of PSE in Cape buffalo killed using succinylcholine, and these incidences were similar to a phenomenon referred to as white muscle capture myopathy, which is often seen in live captured game (Hoffman, 2001b). Furthermore, on a study examining the effects of daytime cropping on warthog (*Phacochoerus africanus*) meat quality, Hoffman (2001b) observed that warthogs, similar to the domestic pigs, are prone to produce PSE condition when exposed to ante-mortem stress.

Animals subjected to prolonged (several hours) ante-mortem stress results in meat that has a higher pH and is dark cutting, more definitively described as DFD (Warriss, 2000). The high pH (pH > 6) results from reduced energy storage in the muscle caused by prolonged ante-mortem stress. The low glycogen concentration leads to decreased production of lactic acid (anaerobic glycolysis) in the muscles; thus, insufficient lactic acid is produced to drop the muscle pH to a normal meat pH of 5.6. The interaction of several factors result in the darker color. The higher pH results in the meat having a greater WHC, which reduces intramuscular water shifts and creates a more compact tissue structure that reflects less light (Lawrie and Ledward, 2006). In addition, less OxyMb forms because less oxygen diffuses into the muscle and there is greater competition for the oxygen from mitochondria that function more efficiently for a longer postmortem time, a process known as oxygen consumption (OC) activity. Consequently, DeoxyMb prevails in DFD meat, resulting in darker appearance (Bendall, 1972; Bendall and Taylor, 1972).

While both DFD and PSE can occur in all species, DFD is more common in red meat species such as beef, lamb and venison, and PSE is more common in pigs (Bartoš et al., 1988; Webb and Casey, 2010). The incidence and biochemistry of DFD have been extensively studied in beef (Bartoš et al., 1993; Hedrick et al., 1959; Holdstock et al., 2014; Viljoen et al., 2002; Wulf et al., 2002), lamb (Hedrick et al., 1961), mutton (Newton and Gill, 1978), chevon (Simela, 2005), and pork (Lewis et al., 1987; O'Neill et al., 2003; Guàrdia et al., 2005). Hoffman (2001a) reported that many game animals tend to produce DFD meat due to prolonged stress during the cropping/harvesting process. Numerous studies on pre-slaughter handling processes of red deer have shown that these animals were also prone to DFD (Wiklund et al., 1995; Malmfors and Wiklund, 1996; Wiklund et al., 1996; Wiklund et al., 2001; Wiklund and Malmfors, 2004). The susceptibility of muscles to DFD differs and is determined mainly by differences in muscle fiber type. Typically stress-prone animals have a greater percentage of white, more anaerobic fiber types compared to stress-resistant pork (Briskey, 1964) and beef (Hunt and Hedrick, 1977a).

Ante-mortem stress not only affects the meat color, it also impacts meat color stability. The high pH of DFD meat minimizes oxidation of Mb leading to an increase in color stability (Gotoh and Shikama, 1974; Ledward, 1985) although the dark color is undesirable to consumers (Faustman and Cassens, 1990; Viljoen et al., 2002). However, the increased color stability is counteracted by a decrease in shelf-life as the higher pH encourages the proliferation of microorganisms (Lawrie and Ledward, 2006; Webb and Casey, 2010; Holdstock et al., 2014). In contrast, the low pH of PSE meat increases the rate of Mb oxidation leading to a decrease in color stability (Gotoh and Shikama, 1974; Ledward, 1985; Faustman and Cassens, 1990; Suman and Joseph, 2013). This accelerated Mb oxidation may be due to accelerated protonation of bound oxygen, which enhances the release of superoxide anions, a known pro-oxidant in meat (Livingston and Brown, 1981). Research on color stability of PSE and DFD pork reported that DFD meat exhibited the highest color stability in comparison to normal and PSE meat, with PSE having the lowest (Zhu and Brewer, 1998). The differences in color stability were attributed to a higher MetMb reducing activity observed for the DFD meat, with the high pH values of the meat maintaining the reducing enzyme activity (Bekhit and Faustman, 2005).

Storage temperature

As with all proteins, Mb is sensitive to temperature fluctuations. The rate at which Mb is oxidized is accelerated with increased temperatures (Brown and Mebine, 1969), and meat discoloration is delayed by lower temperatures (Lanier et al., 1977; Hood, 1980; O'Keeffe and Hood, 1982; Nortje et al., 1986). One of the reasons

for this delay is that the distance from the meat surface at which MetMb is formed is increased due to increased solubility of oxygen in the water present in the meat tissue (Urbin and Wilson, 1958). Additionally, greater the distance the subsurface layer of MetMb is below the surface, the longer it takes for the MetMb to move to the surface (Urbin and Wilson, 1958).

Mb oxidizes more readily at higher temperatures for several reasons. First, higher storage temperatures result in increased reaction rates of prooxidants inherently present within the muscle (Faustman et al., 2010). Second, the dissociation of oxygen from OxyMb is favored due to the decreased solubility of oxygen in the meat matrix at higher temperatures (Urbin and Wilson, 1958), which leads to higher concentrations of DeoxyMb that is more prone to oxidation than OxyMb (O'Keeffe and Hood, 1982). High storage temperatures also increase the activity of oxygen-consuming enzymes in the meat (Ashmore, Parker, and Doerr, 1972; Bendall, 1972; Bendall and Taylor, 1972), enhance microbial growth (Lawrie and Ledward, 2006), and accelerate lipid oxidation (Chaijan, 2008), all of which enhance the discoloration of meat. In total, the degree of discoloration in fresh meat subjected to the same temperature was muscle-dependent (Hood, 1980).

Martin et al. (2013) observed that the ground beef samples stored at 2.3°C discolored more rapidly than those stored at –1.7°C. The accelerated discoloration was attributed to increased microbial growth and lipid oxidation, as both processes produce undesirable by-products, which negatively affect meat color. Numerous studies confirm that increased temperature during storage, processing, and display decrease meat color stability across the species (Hood, 1980; Lanier et al., 1977; Ledward et al., 1986; O'Keeffe and Hood, 1982; Jakobsen and Bertelsen, 2000; Rosenvold and Wiklund, 2011).

The development of bloom is also temperature-dependent. Warmer meat will bloom less as enzyme systems present in the meat outcompete Mb for the oxygen, whereas enzyme systems in colder meat are less active and more conducive to greater Mb oxygenation (Ashmore et al., 1972; Egbert and Cornforth, 1986). Low temperatures (–1.5 to 2°C) are thus recommended for meat quality studies for any species, including domestic and wild ungulates, with respect to blooming, color stability, and microbial shelf-life.

Not all color biochemistry attributes benefit from low temperatures. Vacuum packaged bloomed meat will usually start consuming oxygen and will form MetMb at low oxygen tensions. If the temperature is warm enough (4 to 8°C) the oxygen tension will decrease to near zero, and if a reducing electron is available, the MetMb will be converted to DeoxyMb (Brown and Mebine, 1969). If the temperature is slightly lower, this color conversion will be slow and likely incomplete. Effects of temperature on color biochemistry are relevant to both farmed and wild species of ungulates, but the existing gap in knowledge merits investigation.

Intrinsic factors

Ultimate pH of meat

The acidity of meat is one of the most important factors affecting numerous functional properties of meat, especially meat color and color stability. Research clearly shows that both the rate of pH decline post-mortem and the ultimate pH of the meat critically affect meat color. Much of the earlier discussion for ante-mortem stress is related to both the rate and extent of pH change from approximately 7.2 in living muscle to pH 5.5 to 5.7 in meat, during the post-mortem conversion of muscle to meat (Lawrie and Ledward, 2006). In general, high meat pH results in a darker color, and a lower pH leads to lighter meat color. This is, at least in part, due to the effect of pH on the WHC of meat, along with the fact that meat possessing high and low WHC have darker and lighter colors, respectively.

Oxidation of Mb in beef is accelerated at a low pH (Gotoh and Shikama, 1974; Ledward, 1985) leading to a decrease in color stability. Metmyoglobin reducing ability (MRA) is also influenced by pH, with an increase in pH leading to increased MRA (Ledward, 1971; Stewart et al., 1965). Increased MRA has been linked to an increased color stability (Bekhit and Faustman, 2005), thus meat with a higher pH should be more color stable than meat with a lower pH. Furthermore, the formation of OxyMb is decreased at a high pH as a result of increased and prolonged mitochondrial activity post-mortem resulting in an increased oxygen consumption (Bendall, 1972; Bendall and Taylor, 1972).

Abril et al. (2001) investigated the changes in instrumental color (L^*, a^*, b^*, chroma, and hue) and surface reflectance of beef from two different pH groupings, i.e., pH < 6.1 and pH ≥ 6.1 (DFD meat). Meat pH had a significant effect on all the color variables. Meat with low pH values exhibited high b^* and hue values. The L^* values decreased (meat became darker darker) as the pH values increased, and the reflectance of the beef from the higher pH group (pH ≥ 6.1) was always below that of the lower pH group (pH < 6.1). This trend was also observed in veal by other researchers (Guignot et al., 1994). The lower L^* values observed for the higher pH group is attributed to lower light reflectance and higher absorption

at all wavelengths. The reflectance results indicated that more OxyMb was formed at the surface of beef with pH < 6.1 (better blooming), resulting from decreased mitochondrial function at lower pH values (Bendall, 1972; Bendall and Taylor, 1972). Furthermore, the reflectance results indicated that beef with pH < 6.1 had earlier onset of MetMb formation in comparison to the beef at pH ≥ 6.1. This, along with the higher *b** and hue of beef from the lower pH group confirmed the observations of other researchers, who found that the rate of Mb autoxidation increases and the rate of MetMb reduction decreases at low pH (Bendall and Taylor, 1972; Ledward, 1985).

The pH of meat is very important in determining the color and color stability in fresh meat. The majority of the research regarding pH of muscle has been done with regard to DFD and PSE in beef and pork. Although some research has been done on the effect of pH on the color of venison (Macdougall et al., 1979; Rincker et al., 2006; Wiklund et al., 2006; Farouk et al., 2007; Dahlan and Norfarizan Hanoon, 2008), bison (Dhanda et al., 2002, Dhanda et al., 2003) and game meat (Hoffman et al., 2009b; Hoffman and Laubscher, 2010), only limited literature is available with regard to its effect on color stability. Furthermore, the aforementioned studies, which included the relationship of color and pH in game meat, bison, and venison, have generally been part of broader investigations on meat quality and were not specifically focused on this relationship.

Species

The color of fresh meat is species-dependent (Faustman and Cassens, 1990; Mancini and Hunt, 2005). In pork, lighter flesh, which is greyish-pink in color, is considered acceptable to consumers, whereas fresh meat from ruminant livestock (beef, lamb, and chevon) is darker than pig meat, and a bright cherry-red color is deemed acceptable in these species. Venison and game meat are darker red in appearance than the meat from domestic ungulates (Hoffman, 2000; Daszkiewicz et al., 2011). Since the consumers prefer red meat (such as beef) that is neither too dark nor too pale (Jeremiah et al., 1972), the dark color of game meat may negatively influence the purchasing decisions.

Meat color differences between species is largely due to the differences in Mb content (Warriss et al., 1990; Kranen et al., 1999; Gatellier et al., 2001; Suman and Joseph, 2013), proportion of muscle fiber type (Vestergaard et al., 2000), and intramuscular fat content (Lawrie and Ledward, 2006). In a similar manner, the darker color of venison and game meat is attributed to greater Mb content (Vestergaard et al., 2000; Díaz et al., 2002; Kritzinger et al., 2003; Daszkiewicz et al., 2011), differences in muscle fiber types (Curry et al., 2012; North and Hoffman, 2015) and lower levels of intramuscular fat (Hoffman et al., 2005) in comparison to many domestic species. Furthermore, meat with a higher Mb content also has a higher concentration of iron, which promotes oxidation leading to a decline in the color stability (Farouk et al., 2007; Purchas et al., 2010).

Chevon was darker, redder, and had less intramuscular fat compared to lamb (Babiker et al., 1990). Farouk et al. (2007) observed that beef had higher *L**, *a**, and chroma values (lighter, redder, and more saturated) in comparison with venison when stored at –1.5°C for 4 wk. The darker and less stable color of venison was attributed to its higher concentration of Mb (Young and West, 2001) and prooxidants (Drew and Seman 1987; Stevenson-Barry et al., 1999) in comparison with beef. Similar differences in color were observed between beef, caribou and reindeer (Rincker et al., 2006). The *L** and *a** values for the caribou and reindeer were lower (i.e., darker and less red) than those of the beef, but did not differ from each other. Mb concentrations of the 3 species were different, with beef (7.29 mg/g) having a lower concentration than reindeer (9.79 mg/g) and caribou (8.59 mg/g), which were similar to each other. Thus, the Mb concentration may have been the major reason for the differences in color.

Impala (*Aepyceros melampus*) meat was observed to be darker and redder (*L** = 29.22; *a** = 11.2; Hoffman, 2000) than pork (*L** = 43.7; *a** = 5.44; Fisher et al., 2000). Further studies (Hoffman et al., 2005) reported more Mb in impala meat (7.25 to 7.50 mg/g) compared with beef (5.80 mg/g) and offered this as the reason for the dark color observed in game meat. However, Bartoň et al. (2014) observed that eland (*Taurotragus oryx*) meat was lighter (*L** = 36.3) than beef (*L** = 41.0). These findings were similar to other studies that reported that beef was lighter in comparison to meat from bison (Koch et al., 1995), reindeer and caribou (Rincker et al., 2006), as well as red deer (Farouk et al., 2007).

A meat quality comparison of impala and kudu (*Tragelaphus strepsiceros*) documented that kudu meat had significantly higher *L**, *a**, *b**, and chroma values than impala meat (Hoffman et al., 2009b). However, the higher *a** values for kudu meat were not due to the Mb content as no significant differences were observed between the 2 species. Interestingly, hue angle did not differ between kudu and impala meats (Hoffman et al., 2009b), but was higher than values reported for meat from springbok (Hoffman et al., 2007) and black and blue wildebeest (Van Schalkwyk, 2004). Larger hue angle values indicate lower redness and more MetMb content on the meat surfaces (American Meat Science Association, 2012).

Volpelli et al. (2002) described that venison meat was characterized by low *L** values (below 40), high *a** values, and low *b** values, which are indicative of the dark red color. The darker color of game animals may also be attributed to stress from poor cropping methods resulting in DFD meat (Von La Chevallerie and van Zyl, 1971; Von La Chevallerie, 1972; Scanga et al., 1998; Hoffman, 2001a). The higher Mb content and resulting darker meat found in game meat and venison are most likely due to higher levels of physical activity (Vestergaard et al., 2000; Díaz et al., 2002), with wild ungulates being more active than domestic ungulates (Hoffman, 2000). However, this is not necessarily the case for all wild ungulates. The meat from mountain reedbuck (*Redunca fulvorufula*) was minimally darker than that of beef, which could be attributed to the behavior of the mountain reedbuck, which only frequents small territories and is relatively inactive (Hoffman et al., 2008). Although significant literature is available on the species-specific color differences in meats from livestock, limited research has been done on the color stability of various game and venison species.

Breed

Within a species, breeds will also differ in color and color stability due to differences in the biochemistry of their muscles. Lanari and Cassens (1991) observed that beef from Holstein cattle was less color stable than beef from crossbred animals. They attributed the differences to variations in mitochondrial respiration activities among breeds; those with the highest oxygen consumption rates (Holstein) were the most color labile. These results are partially supported by other studies (O'Keeffe and Hood, 1982; Renerre and Labas, 1987; Echevarne et al., 1990), which reported that beef muscles with higher reducing activities exhibited higher color stability. Similarly, meat from Parda de Montaña cattle breed was more color stable than meat from Pirenaica breeds, although no reasons for the difference were given (Ripoll et al., 2014).

Differences in initial color were observed for 5 different Spanish cattle breeds (Insausti et al., 1999); beef from Morucha breed was redder than the other 4 breeds. The redder meat in Morucha cattle was possibly due to a higher Mb content (Demos and Mandigo, 1996) resulting from earlier development (Renerre and Valin, 1979) and greater physical activity associated with this breed (Kempster, 1981) compared to the other breeds studied. Furthermore, Morucha breed was the least color stable of the breeds, most likely also due its higher Mb concentration (Insausti et al., 1999). Other authors also reported differences in Mb content and reflectance for different cattle breeds, with lower Mb content and higher light reflectance for Limousine, Charolais, Romangola, and Blonde d'Aquitane cattle than for Simmental, White Cattle, Hereford and Chianina crossbreds (Liboriussen et al., 1977). Further, instrumental color and Mb content were suggested as potential parameters to characterize beef from different breeds (Insausti et al., 1999). Conversely, no differences were observed for the meat color or color stability between Limousine and Retinta breeds (Avilés et al., 2015).

Kadim et al. (2004b) investigated the meat quality differences between 4 muscles (longissimus, biceps femoris, semitendinosus, and semimembranosus) of 3 different Omani goat breeds, Batina, Dhofari, and Jabal Khaddar. No differences were observed between the *a** and *b** values among breeds for any of the muscles, whereas differences in *L** were observed, with the longissimus of the Jabal Khaddar goats being lighter than those of the Batina and Dhofari, and the semimembranosus of the Jabal Khaddar and Dhofari being lighter than their counterparts from Batina. Thus, both breed and muscle source influenced the color of goat meat. Other authors have also documented differences in muscle color among goat breeds (Dhanda et al., 1999).

Variations in color among pig breeds have also been studied. Lindahl et al. (2001) investigated the color differences between the longissimus and biceps femoris of purebred Hampshire, Swedish Landrace and Swedish Yorkshire pigs, and observed that the longissimus of the Hampshire breed was redder in comparison to the other 2 breeds. The longissimus and biceps femoris of the Hampshire breed were also more yellow than their counterparts from the other 2 breeds, and the differences in color were attributed to the differences in glycogen content in the muscles. Hampshire pigs had higher levels of glycogen in their muscles, lower protein and higher water-to-protein ratios compared with other breeds, which may have influenced the meat color (Sellier and Monin, 1994).

Meat color differences were also observed for Celta pigs cross-bred with Duroc and Landrace breeds (Franco and Lorenzo, 2014); the *L** values for Celta pigs were lower than for the Celta × Landrace crossbred, whereas the *L** values for Celta × Duroc did not differ from the other 2 breeds. The *a** values for Celta were the highest, with the *a** values for the cross-bred animals (Celta × Landrace; Celta × Duroc) not differing from each other. The differences in redness were attributed to differences in Mb content between the breeds, with higher Mb contents linked to higher redness. Other studies have also noted difference in in-

strumental color among different pig breeds (Gjerlaug-Enger et al., 2010; Li et al., 2013; Shen et al., 2014).

Differences in color between lamb breeds have also been recorded (Hopkins and Fogarty, 1998; Martínez-Cerezo et al., 2005; Teixeira et al., 2005). Martínez-Cerezo et al. (2005) compared the surface color of three different Spanish lamb breeds (Rasa Aragonesa, Churra, and Spanish merino) and observed that the *L** values for the Churra were higher than the other 2 breeds. Furthermore, these authors observed that the Spanish merino had the highest *a** values and the Rasa Aragonesa had the highest *b** values.

Unlike domestic ungulates, where several different breeds exist within each species, no breeds exist for wild ungulates, but only sub-species. Breed differences definitely play a crucial role in muscle color and color stability in domestic ungulate species, and should be considered as a production parameter. From this perspective, crossbreeding within a species may be considered as a potential option for improving meat color and color stability in domestic species.

Animal-to-animal variation

Although variations in meat color exist among different animals within a species and breed, very little research has been conducted on the effect of animal-to-animal variation on color. King et al. (2010) reported that there was substantial animal-to-animal variation (within a species and breed) in beef color and that animal-to-animal differences played a larger role in the capacity of the muscle to maintain its color, rather than in its initial color. Furthermore, these authors highlighted the existence of opportunities to improve color stability through genetic selection. In contrast, Newcom et al. (2004) reported that in pork, genetics played a larger role in the initial color. The initial oxygen consumption and reducing capacity contributed to variations in beef color stability between animals (King et al., 2011). However, earlier research on beef found that muscle type (Hood, 1980; Renerre and Labas, 1987) had a greater effect on color stability than the animal-to-animal variation. Interestingly, the results of King et al. (2011) indicated that the influence of animal-to-animal variation was consistent across beef muscles. Therefore, strategies to improve beef color stability would thus be consistent across all muscles.

Canto et al. (2015) evaluated differences in the sarcoplasmic proteome of beef longissimus steaks from carcasses demonstrating variations in color stability and correlated color stability attributes to differentially abundant proteome components. The results indicated that animal-to-animal variation could be explained by differences in the sarcoplasmic proteome profile. An excess of glycolytic enzymes in color-stable steaks was found to contribute to the improved color stability, most likely due to the regeneration of NADH post-mortem. Furthermore, in color-labile muscles, the decrease in color stability was attributed to possible post-translational modification of Mb.

Animal-to-animal variation may have an even greater effect on color stability in wild ungulates due to their greater genetic variations compared to that of domestic species. There are numerous knowledge gaps for animal-to-animal effects on game meat color and color stability that merit investigation.

Sex

In general, the meat from intact male animals is darker (Seideman et al., 1982) than meat from females and castrated males, which is attributed to higher concentrations of Mb in intact males likely due to greater levels of physical activity. The higher Mb concentrations found in males could contribute to a decrease in color stability (Insausti et al., 1999). However, studies regarding the effects of sex on meat color are inconclusive.

Greater *L**, *a**, *b**, and chroma values were reported by Kim et al. (2003) for beef from steers in comparison with beef from bulls and cows. Interestingly, in the same study, no significant differences were reported for *a**, *b**, and chroma between cows and bulls. Węglarz (2010) noted differences in meat color between cows and bulls, with cows having higher *b** and lower hue values than bulls.

In pork, differences in meat color between gilts and castrates have been documented in several studies (Warriss et al., 1990; Jeremiah et al., 1999; Franco and Lorenzo, 2014), while other investigations found no differences (Unruh et al., 1996; Lindahl et al., 2001; Li et al., 2013). Warriss et al. (1990) observed greater *a** values and lower hue values in gilts compared to castrates, whereas no differences were noticed in *L**, *b**, and chroma values.

Simela et al. (2004) reported that meat from intact male goats had lower *a** values than females and castrates, and the chroma of the intact males and females was lower than that of the castrates. Teixeira et al. (2005) documented that male lambs had higher *L** values than females, but there were no significant differences for *a** and *b** values.

Hoffman et al. (2008) observed no differences in the color of longissimus muscles from male and female mountain reedbuck (*Redunca fulvorufula*). These findings are congruent with those on impala (*Aepyceros melampus*) and kudu (*Tragelaphus strepsiceros*), where

no color differences were observed between male and female animals (Hoffman et al., 2009b). The lack of differences in color between male and female mountain reedbuck, impala and kudu may be due to no differences in the Mb content and physical activity between the males and females in these species (Hoffman et al., 2009b). Similarly, no color differences were observed between male and female roe deer (Daszkiewicz et al., 2009; Purchas et al., 2010; Daszkiewicz et al., 2012). However, differences in meat color have been observed for gemsbok (*Oryx gazella*), with females having lower *L**, *b**, hue and chroma values (Hoffman and Laubscher, 2010), which contradicts the hypothesis that males have darker muscle than females. Furthermore, differences in sex were observed for springbok (*Antidorcas marsupialis*), with females having greater *a** and chroma values possibly due to higher pH values than in the male counterparts (Hoffman et al., 2007). These disagreements could be possibly due to the effect of species and their biology as well as the variations in physical activities of different species.

Animal age

The concentration of Mb in meat increases as animal age increases (Onyango et al., 1998; Kim et al., 2012; Humada et al., 2014; Cho et al., 2015). Myoglobin concentration affects the perceived meat color (Warriss et al., 1990; Kranen et al., 1999; Gatellier et al., 2001) such that the older animals had darker (lower *L** values) and redder (higher *a** values) meat. The increase in Mb may also lead to a decrease in color stability with age (Insausti et al., 1999). Furthermore, fat deposits also tend to become more yellow in color over age due to an increase in carotenoid deposits (Lawrie and Ledward, 2006), which may also affect the perceived color of meat.

Dhanda et al. (1999) compared kid and goat meat. As animal age increased, Mb concentration and *a** values of lean increased and *L** and *b** decreased. Thus, the meat became darker, redder, and less yellow. Although an increase in fat yellowness was observed in older animals in the same study, these measurements were done on subcutaneous fat and would thus not necessarily give an indication of the color change on lean meat. Other researchers have also documented an increase in subcutaneous fat yellowness with age in goats (Rao et al., 1988).

Domínguez et al. (2015) reported that the *L** values for foals decreased as age increased from 8 to 11 mo; however, the darkening of the muscle was not accompanied by an increase in Mb concentration or any changes in *a** and *b** values during that time span. In partial agreement, a comparison of instrumental color and heme iron content of foals aged 9 and 12 mo found no differences (Franco et al., 2011)

Jacob et al. (2007) found a decrease in color stability in lamb with age. This was attributed to an increase in Mb concentration with age suggesting that the muscles from the older lambs were more oxidative in nature than those of the younger lambs. The increase in Mb level with age in lamb meat was consistent with findings from other studies (Pethick et al., 2005; Kim et al., 2012). Kim et al. (2012) noted higher *L** and lower *a** values for younger lambs (3 to 4 mo) in comparison to older lambs (10 to 11 mo), and these differences were attributed to the higher Mb concentrations found in the older lambs.

A study conducted by Sookhareea et al. (1995) using three different muscles (longissimus, semimembranosus, and semitendinosus) of male deer found that *L** and *a** values increased and *b** values decreased for all muscles as animal age increased. The increase in *L** values with age is contradictory to what would be expected by an increase in Mb concentration. The authors attributed the increase in lightness to a lower pH and slower cooling of the heavier carcasses from older animals. Differences in color were also noted for sub-adult and adult male kudu and impala (Hoffman et al., 2009a). Sub-adult males (below 34 mo age for kudu; below 30 mo for impala) had higher *L** values and correspondingly lower Mb concentrations in comparison to adult males (above 34 mo for kudu; above 30 mo for impala). Similarly, color differences between adult (2 to 5 yr age) and sub-adult (1 to 2 yr age) springbok have also been observed (Hoffman et al., 2007). Adult springbok had lower *L**, *a**, and chroma values and, higher hue angle values in comparison to subadults; but no differences in *b** values were observed. Conversely, Volpelli et al. (2003) found no differences in color between male deer aged 18 and 30 mo.

The effect of age on beef color has been reported in several studies. Tang, Ma, and Liang (2010) observed lower *L**, *a**, and chroma values for older (9 to 10 yr) Yanbian yellow cattle compared to younger animals (1.5 to 6 yr). Cho et al. (2015), observed lower *L**, *a**, *b**, and chroma values and decreased color stability for older Korean Hanwoo animals. In the latter study, higher Mb concentrations and increased lipid oxidation with age were given as the reasons for a lower *L** values and decreased color stability, respectively.

Muscle source

A multitude of investigations have documented the muscle-specific variations on color and color stability of fresh beef (Ledward, 1971; Hunt and Hedrick,

1977a; O'Keeffe and Hood, 1982; Renerre and Labas, 1987; McKenna et al., 2005; Von Seggern et al., 2005; Jeong et al., 2009; Kim et al., 2009; Joseph et al., 2012; Canto et al., 2016). Intermuscular variations critically influence the color shelf-life of packaged fresh beef, with some muscles discoloring at a faster rate than the others (Hood, 1980). The muscle-specific color phenomena could be attributed to the differences in the relative proportions of fiber types present in the muscle (Hunt and Hedrick, 1977a) as well as the oxidative and reductive capacities of the post-mortem muscles (Bekhit and Faustman, 2005; Suman and Nair, 2017).

The fiber type influences the amount of Mb present, the oxidative capacity of the muscle, and both the rate of pH decline and the extent of pH change post-mortem, all of which influence color and color stability (Hunt and Hedrick, 1977a; Kim et al., 2014). In mammals, muscle fiber types are divided into four groups– type I, and types IIA, IIX and IIB. The fiber types are categorized according to the energy source utilized, metabolic pathways, and contraction rate (Lawrie and Ledward, 2006; Curry et al., 2012). Type I fibers also referred to as slow-twitch oxidative fibers. These fibers are smaller in size, slow contracting (Schiaffino and Reggiani, 1996; Bottinelli, 2001), contain large numbers of mitochondria and aerobically metabolize fat, glucose and glycogen to produce ATP and, are highly resistant to fatigue (Pette, 1985). Type IIA also referred to as fast-twitch oxidative fibers, which are fast contracting, contain relatively large numbers of mitochondria and can produce ATP aerobically and anaerobically. The ability to use both aerobic and anaerobic metabolism to produce ATP makes these fibers resistant to fatigue (Pette, 1985; Schiaffino and Reggiani, 1996). Type IIX fibers, also known as fast-twitch glycolytic fibers, are fast contracting (faster than type IIA), contain few mitochondria, primarily metabolize glucose, and glycogen anaerobically for ATP production and, fatigue rapidly (Pette, 1985). Type IIB fibers are also fast-twitch glycolytic, contain low levels of mitochondria, are mostly anaerobic, and extremely susceptible to fatigue (Warriss, 2000). They also have a lower oxidative capacity than type IIX fibers (Greenwood et al., 2007; Lefaucheur, 2010; Curry et al., 2012).

Fresh meat color and color stability are influenced by the relative proportions of the muscle fiber types. Muscles with higher proportion of oxidative fibers (type I) are a darker, deep red color in comparison to those with higher proportion of glycolytic fibers (type IIX) due to a higher Mb content (Hunt and Hedrick, 1977a; Kirchofer et al., 2002). Oxidative beef muscles (with majority oxidative fibers; e.g., semimembranosus) are more prone to oxidation and thus have a faster rate of discoloration than the glycolytic muscles (with majority glycolytic fires; e.g., semitendinosus) from the same carcasses (O'Keeffe and Hood 1982; Renerre and Labas, 1987). Oxidative muscles are thus, in general, darker and less color stable than glycolytic muscles.

Hunt and Hedrick (1977b, c) studied various chemical, physical, histological and sensory properties of beef that were categorized as PSE (pale, soft and exudative), NOR (normal color texture and exudativeness), NSE (normal in color, but soft and exudative) and DC (dark-cutting) beef. Of these groups, the PSE and DC were on opposite ends of almost all qualitative and quantitative traits. The NSE was intermediate but was more PSE-like with greater processing losses compared to the NOR group.

A study on the effects of the diet/production system (intensive feedlot vs. extensive grazing) on the muscle fiber characteristics and beef color concluded that the difference in physical activity had a greater effect on the meat color than the diet associated with that production system (Vestergaard et al., 2000). Beef animals in extensive production systems have higher levels of physical activity than those in the intensive production systems (Vestergaard et al., 2000), which leads to higher ratios of slow-twitch muscle fibers (Aalhus and Price, 1991). Increased physical activity leads to an increase in type IIA (fast-twitch, oxidative and glycolytic) and a decrease in type IIB (fast-twitch, glycolytic) muscle fibers in young bulls (Van Vooren et al., 1992). In lambs and pigs, type I (slow-twitch, glycolytic) muscle increased with an increase in physical activity (Aalhus and Price, 1991; Petersen et al., 1998). The results indicated that the semitendinosus and longissimus had higher proportions of type IIB muscle fibers in comparison to type I and IIA, and the supraspinatus had higher proportions of type I muscle fibers. Correspondingly, the supraspinatus had the highest Mb concentration followed by the longissimus and then the semitendinosus. Interestingly, the supraspinatus did not have the highest a^* value despite having the highest percentage of type I muscle fibers and Mb content. The semitendinosus has a similar a^* value to that of the supraspinatus, with the longissimus having the highest a^* value.

Renerre and Labas (1987) investigated the color stability of 3 beef muscles (i.e., tensor fasciae latae, diaphragm medialis, and psoas major), and the results indicated that the tensor fasciae latae was the most color stable, the diaphragm medialis the most unstable in color, and the PM had an intermediate color stability. Furthermore, these results suggested a relationship between muscle fiber type composition and color stability (Renerre and Labas, 1987). The tensor fasciae latae

is mainly composed of fast-twitch white muscle fibers (glycolytic), the diaphragm medialis is of slow-twitch red (oxidative), and psoas major is predominantly of fast-twitch red (intermediate). The muscles with the highest oxidative activity (i.e., with the most oxidative muscle fiber types) had the poorest color stability. Similarly, the high color stability of the tensor fasciae latae was also noted by McKenna et al. (2005).

Several studies have documented the difference between the color stabilities of the beef longissimus and psoas major muscles (O'Keeffe and Hood, 1982; Madhavi and Carpenter, 1993; McKenna et al., 2005; Seyfert et al., 2006; Seyfert et al., 2007; Kim et al., 2009; Mancini et al., 2009; Joseph et al., 2012; Canto et al., 2016). This observed color difference has been attributed to variations in the proportions of muscle fibers present in these 2 muscles (Seyfert et al., 2006). Beef longissimus has a higher proportion of type IIA fibers than type I fibers, whereas psoas major is composed primarily of type I fibers, and this explains the variations in color stability between these muscles.

Although the influence of fiber type on the color of venison and game meat has not been investigated, research on muscle fiber types present in various muscles of these species has been conducted. Studies on venison (deer and reindeer) species (Kiessling and Kiessling, 1984; Essén-Gustavsson and Rehbinder, 1985) and game (blesbok, kudu, springbok, black and blue wildebeest) meat (Kohn et al. 2011; Curry et al., 2012; North, 2014) have reported that muscles from venison and game contained the proportions of muscle fiber types in descending order of type IIX > type IIA > type I. These findings are contradictory to the logical expectation that the dark red color associated with these species would suggest high proportions of type I muscle fibers (Curry et al., 2012). These findings suggested that the relationship between muscle fiber type and color biochemistry are different in livestock and game species.

The oxidative and reductive capacities are important in fresh meat color and color stability (Bekhit and Faustman, 2005; Suman and Nair, 2017). The oxidative capacity is generally measured by as OC or as oxygen consumption rate (OCR) if a time-related rate is calculated, whereas the reductive capacity is estimated by MRA. The OC is determined by the mitochondrial respiration activity within the meat. The mitochondria will compete with Mb for available oxygen, decreasing the quantity available to bind to Mb to form OxyMb and decreasing the depth of OxyMb layer (Bendall and Taylor, 1972). Since OC is dependent on residual mitochondrial activity, it is linked to muscle fiber type. Oxidative fibers contain more mitochondria and would thus have higher OCR than glycolytic fibers (Beecher et al., 1965; Beecher et al., 1969; Jeong et al., 2009). This, in part, explains the low color stability of muscles with higher proportions of oxidative fibers. The relationship between OCR and oxygen penetration depth is influenced by muscle type (Bendall and Taylor, 1972; Macdougall and Taylor, 1975; O'Keeffe and Hood, 1982; Renerre and Labas, 1987; Lanari and Cassens, 1991; Madhavi and Carpenter, 1993; McKenna et al., 2005). Conversely, MRA refers to the inherent ability of meat to reduce MetMb back to ferrous DeoxyMb, which can subsequently be re-oxygenated to OxyMb and thereby sustaining the color stability (Madhavi and Carpenter, 1993). Thus, higher levels of MRA in meat results in better color stability, and the pathway responsible for this reduction is primarily enzymatic in nature with NADH as cofactor. These enzymatic systems are in general consist of metmyoglobin reductases, and mitochondria and sub-mitochondrial particles play a critical role in MetMb reduction (Giddings and Hultin, 1974).

The importance of the OC and MRA of muscles in color development and color stability has been noted (Madhavi and Carpenter, 1993; Bekhit and Faustman, 2005; Mancini and Hunt, 2005; Suman and Nair, 2017). However, the relative contribution of MRA and OC to the color stability of muscles had been greatly disputed. While some researchers argue that MRA within the muscle is the principal determinant of muscle color stability (Ledward, 1971), others have observed that the reducing activity is of very limited consequence and that OC has more influence on color stability (Atkinson and Follett, 1973; O'Keeffe and Hood, 1982; Renerre and Labas, 1987). Nevertheless, evidence has shown that both reducing activity and OC have an influence on the color stability of muscles (Madhavi and Carpenter, 1993). In contrast, other researchers have suggested that low OC negatively affects color stability as mitochondrial respiration is required to replenish the NADH required for MRA (Sammel et al., 2002).

A relationship between reducing activity and OCR, which could explain the differences in color stability between beef muscles, has been proposed earlier (McKenna et al., 2005; Atkinson and Follett 1973); these authors argued that the OCR influences color stability at a greater degree relative to the reducing activity within a muscle. In muscles with low OCR and low MRA (e.g., adductor), the reducing activity cannot compete with the oxidative stress imposed by the OCR and the color stability is decreased. Muscles with high MRA relative to low OCR (e.g., tensor fascia latae) have higher color stabilities as the reducing activity can compensate for the oxidative stress imposed by the OCR.

Seyfert et al. (2006) investigated the color stability of 4 beef muscles and observed that the color stabilities of the muscles ranked as follows: longissimus (most stable) > semitendinosus > semimembranosus > psoas major (least stable). These authors linked the differences in color stability to differences in muscle fiber type, OCR, and MRA. The most color-stable muscles were found to have high proportions of white, glycolytic fiber types, lower OCR and higher MRA, whereas the least stable muscles had high proportion of red, oxidative fiber types.

Differential color stability of the beef longissimus (color-stable) and psoas major (color-labile) makes these 2 muscles ideal models to investigate the biochemical basis for color stability. Investigations by O'Keeffe and Hood (1982) indicated that the beef psoas major had a higher OCR and lower MRA in comparison to the longissimus. The differences in the color stabilities between these 2 beef muscles were further attributed to the differences in the demand for oxygen by the various respiratory systems present in the muscle post-mortem, with those of the psoas major having higher oxygen demand than the systems in the longissimus. Other researchers have also reported the differences in color stabilities between these beef muscles, which were attributed to differences in OC and/or MRA activity (Mancini et al., 2008; Jeong et al., 2009; Kim et al., 2009; Canto et al., 2016) as well as the abundance of antioxidant proteins (Joseph et al., 2012).

Compared to the extensive studies on the influence of muscle source on color attributes in livestock, only limited studies examined this phenomena in game meat. Recently, Neethling et al. (2016) investigated muscle-specificity in fresh meat from blesbok (*Damaliscus pygargus phillipsi*) and observed that the blesbok infraspinatus muscle is more color-stable than the longissimus and biceps femoris counterparts. This observation is very different from the ones previously reported for fresh beef and suggested that the game species have a unique biology and that the influence of muscle source on color stability is species-dependent.

Lipid oxidation

Correlations between lipid oxidation and Mb oxidation in meat have been noted in muscle foods (Faustman and Cassens, 1990; Faustman et al., 2010). Myoglobin and lipid stabilities are interdependent; oxidation of one entity will compromise the stability of the other (Baron and Andersen, 2002; Chaijan, 2008). The molecular basis of lipid oxidation-induced Mb oxidation has been studied extensively, and the results indicated that the highly reactive products of lipid oxidation accelerate Mb oxidation (Faustman et al., 2010). The reactive by-products of lipid oxidation include α, β-unsaturated aldehydes, which are able to form covalent adducts with red meat myoglobins, accelerating meat discoloration (Faustman et al., 1999; Alderton et al., 2003; Suman et al., 2007). Alternatively, Mb has the ability to initiate lipid oxidation when oxygen is released from OxyMb resulting in the production of ferric (Fe^{3+}) MetMb and superoxide anion radicals. Subsequently, the MetMb is oxidized to the highly reactive ferryl (Fe^{4+}) Mb (Richards and Hultin, 2002).

McKenna et al. (2005) evaluated lipid oxidation in 19 beef muscles and found that the least color stable muscles also had the highest lipid oxidation reiterating the relationship between lipid oxidation and color stability. Conversely, Jeong et al. (2009) found no differences in lipid oxidation between beef muscles of varying color stabilities. Various factors affect the rate of lipid oxidation including the degree of unsaturation of the fatty acids, light, oxygen concentration, temperature, anti- and pro-oxidants (naturally present or added to the diet), and the presence of enzymes (Chaijan, 2008).

Meat from animals with high levels of PUFA is more prone to lipid oxidation and discoloration (Morrissey et al., 1998; Nute et al., 2007). Williams et al. (1983) reported the phospholipid concentrations in various meat species and noted that meat from antelope (960.9 mg/100 g), deer (967.4 mg/100 g) and elk (707.5 mg/100 g) had much higher phospholipid concentrations than beef (502.3 mg/100 g). The higher PUFA concentrations observed in venison/wild game could contribute to the rapid discoloration in post-mortem muscles (Stevenson-Barry et al., 1999). The level of PUFA in meat can be affected by diet, and grazing/pasture-based diets lead to higher levels of PUFA than concentrate-based diets (Wood et al., 2004). Thus, it is logical to expect that meat from animals reared on grazing/pasture would be more prone to lipid oxidation and discoloration. However, Wiklund et al. (2006) observed better color stability in red deer meat from grazing animals compared to concentrate-fed animals despite the grazing animals having higher levels of PUFA. This discrepancy was attributed to the higher levels of vitamin E in the meat of grazing animals, which results from their diet. This argument is further strengthened by the work of Ponnampalam et al. (2012), who investigated the joint relationship between vitamin E, heme iron and PUFA on color stability of lamb; the study reported that the level of vitamin E and heme iron in the meat influenced color stability at a greater degree than the level of PUFA. Thus, investigating the relationship between color stability and lipid oxidation, without measuring the antioxidant and heme iron content, may cause misleading conclusions.

From the aforementioned standpoint, an antioxidant that received the most attention with respect to meat color and lipid oxidation is vitamin E. Numerous researchers have investigated its effect of lipid oxidation and color stability in meat (Faustman et al., 1998; Jakobsen and Bertelsen, 2000; Gatellier et al., 2001; Luciano et al., 2009). Dietary supplementation of vitamin E is affective as a color-stabilizer at different concentrations in muscles from different species; vitamin E levels of 2.95 to 3.0 mg/kg were reported to minimize lipid oxidation in lamb (Jose et al., 2008; Ponnampalam et al., 2012), whereas 7 to 9 mg/kg was reported for venison (Okabe et al., 2002). However, vitamin E is not equally effective to improve color of meat from all species; the effect of vitamin E supplementation on color stability is more distinct in beef (Faustman et al., 1989; Arnold et al., 1992) compared to pork (Cannon et al., 1996; Phillips et al., 2001). An explanation for this difference was provided by Suman et al. (2007), who observed that pork Mb is less liable to alkylation by α, β-unsaturated aldehydes than beef due to fewer nucleophilic histidine residues being present in pork Mb. Thus, pork Mb is less susceptible to the lipid oxidation-induced oxidation than beef Mb. Other research has also reported the higher susceptibility of beef to lipid oxidation in comparison to pork (Kim et al., 2002; Min et al., 2008; Ramanathan et al., 2009).

Antioxidants proteins have the ability to delay or inhibit lipid oxidation and thus increase color stability in meat. The intermuscular variations observed in the color stability of beef longissimus (color-stable) and psoas major (color-labile) muscles (McKenna et al., 2005, Seyfert et al., 2007; Mancini et al., 2009) have been attributed to higher levels of antioxidant proteins in color stable muscles (Joseph et al., 2012).

Conversely, prooxidants initiate/accelerate lipid oxidation (Chaijan, 2008). There are several naturally occurring prooxidants in red meats, including iron and copper (Lawrie and Ledward, 2006). Iron is the most notable and occurs as either heme (associated with Mb) or non-heme iron. Liu and Watts (1970) demonstrated that both heme iron and non-heme iron accelerate lipid oxidation. Non-heme iron, in particular, has been implicated as a catalyst for lipid oxidation (Chen et al., 1984), and thus muscles with high levels non-heme iron would exhibit decreased color stability. High levels of heme iron have been noted in deer (24 μg per gram; Wiklund et al., 2006) in comparison to beef (19 μg per gram; Berge et al., 1993). As with PUFA, the higher heme iron concentrations reported in venison/wild game could contribute to the rapid discoloration (Stevenson-Barry et al., 1999).

The high PUFA and prooxidant concentrations in venison and game meat could explain their increased susceptibility to discoloration. Processing methods that inhibit/minimize lipid oxidation may thus contribute to increasing the color stability and marketability of venison and game meat. Although prodigious quantities of literature are available on the effect of lipid oxidation on color stability in livestock meat, research is notably lacking in venison and game species.

Conclusions

Color and color stability are critical to the economic competitiveness of meat industry as they determine the consumers' purchase intent and marketability of retail fresh meat. The exogenous and endogenous factors affecting color and color stability are not mutually exclusive, but are often interrelated. Furthermore, many of these factors are species-, breed-, and muscle-specific in nature. While significant amount of scientific information is available on color of fresh meats from livestock, literature on color biochemistry of game meat and venison is conspicuously lacking. Researchers also often group wild ungulate species together, assuming that they will have similar color and color stabilities, while these species may have color attributes as varying as those noted in conventional livestock.

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