Relationship between trained sensory and objective measured meat quality attributes in crossbred Canadian beef cattle after 3- and 29-days post-mortem aging

by

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Abstract:

Meat quality attributes are pivotal for the beef industry. Studies across Canada showed major beef quality concerns originate from inconsistency of palatability attributes. To improve these traits genetically, they should be standardly measured, their (co)variance components and genetic parameters estimated. There are different approaches for measuring meat quality traits including objective (using Warner Bratzler Shear Force -WBSF- or color measurements) and subjective (i.e., trained sensory panel scoring) methods. Subjective methods for sensory assessment proved to closely describe eating experience of meat that influence meat purchasing preference. But on the downside these traits are time consuming, labor intensive and costly to measure while objective measurements are not. In this study, as a potential alternative for replacing sensory panel evaluation with objective methods, data for both sets of traits after 3- and 29-days post-mortem aging for 1,200 multibreed beef cattle were collected and analyzed.

First, associations between meat quality traits and sensory panel scoring were investigated. Pearson phenotypic correlations, variance components (using univariate model), and genetic correlation calculation (using a two-trait model) were estimated. Fixed effects (contemporary grouping, sex, breed composition and slaughter age) and a random additive effect were fitted into the models. Results indicated that phenotypic correlations between subjective and objective measured traits were mostly weak (< 0.3). This suggests that meat quality attributes are changing between day 3 and 29 post-mortem and early assessment of these traits are not good indicators of the final values. Heritability estimates at day 3 and 29 post-mortem for overall tenderness (OT), overall palatability (OP), WBSF and fat content were moderate to high. These estimates suggested the possibility of improvement through animal breeding for these traits. Genetic correlations were strong (> 0.6) between WBSF and OT, OP, connective tissue (CT) and flavor

intensity (FI), as well as fat content with FI, off-flavor (OF) and OP. This was also the case for OT with OF and OP. Similarly, OP was highly correlated with FI and sustained juiciness (SJ), as well as CT with OT, FI, OT and OP. These strong genetic correlations suggests that there are potentially common genes impacting these traits and in a selective breeding program they should be considered for genetic improvement.

Next, genetic parameters for color attributes (lightness, Hue and Chroma) and their associations with sensory panel scoring traits were studied. Results indicated weak phenotypic Pearson's correlations between sensory attributes and color indices (<0.3), implying low consistency between these traits at day 3 and 29 post-mortem. Genetic parameter estimation showed that lightness and Hue were highly heritable. These results indicate that the lightness and Hue of beef, after 3 and 29 days of aging, can be targeted through breeding programs for improvement. Trend analysis evaluated color attributes during retail display at different shelf-life days (days 0, 2 and 4). Color measurements during retail display (day 0, 2 and 4) had negligible heritability estimates (< 0.1). The results for retail color attributes indicate these traits are mostly affected by environmental factors rather than additive genetic effect. Genetic correlation estimations revealed that lightness was moderately correlated to CT, and Chroma was strongly correlated to CT, OF and OP, and moderately correlated to OT and FI. The fact that color indices are genetically correlated to palatability attributes indicates some level of pleiotropy for these traits. Color retail display, lightness, Hue and Chroma at days 0, 2 and 4 of shelf-life, had significant decline from day 0 to 4 as well as day 2 to 4 (p-value <0.001). This could help to find the optimum point (day 2) of display for beef meat before the product loses its appeal due to discoloration as the largest decrease in color quality happens between day 2 to 4.

Overall, meat quality attributes are not consistent through time and early measurements cannot be considered as good indicators for changes over time. Some of these traits were highly heritable implying the chance of genetic improvement with selective breeding. Strong genetic correlations between sensory and objective measured traits shows possible pleiotropic effects. We suggest that WBSF, fat content, lightness and Hue as objective measured traits are good indicators for sensory attributes. These results should be considered when designing genetic improvement strategies of meat quality attributes in Canadian crossbred beef cattle.

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List of abbreviations

a*: Color index; green to red

ALA: α-linoleic acid

b*: Color index; blue to yellow

BC: Breed composition

CG: Contemporary grouping

Chroma: Chroma of meat's color; saturation of the color

CSA: Cross-sectional areas

CT: Connective tissue

ECM: Extracellular matrix

Fat: Fat content

FI: Flavor intensity

GDP: Gross Domestic Product

GWAS: Genome wide association studies

h^2: Heritability in a narrow sense

HSPs: Heat Shock Proteins

Hue: Hue of meat's color

IMF: Intramuscular fat

L*: Color index; brightness of the meat

LA: Linoleic acid

MUFA: Monounsaturated fatty acids

NL: Neutral lipid

OF: Off-flavor intensity

OP: Overall palatability

OT: Overall tenderness

PGs: Proteoglycans

PL: Phospholipid

PUFA: Polyunsaturated fatty acid

SE: Standard error

SFA: Saturated fatty acids

SJ: Sustainable juiciness

Sla. age: Slaughter age

SNP: Single nucleotide polymorphism

σ_a^2: Additive genetic variance

σ_e^2: Residual variance

WBSF: Warner-Bratzler shear force

WHC: Water holding capacity

Chapter 1. General Introduction and literature review

1.1 Introduction

Meat has been a basic dietary component for man for several millennia. Early humans gathered and hunted large animals for sustenance and survival. Regarding animal domestication, sheep, and goat and after some time cattle were the first animals that people domesticated to use their products such as meat, milk, leather, and wool. As communities reshaped to more sedentary and modern lifestyles, the demand for these products increased. Meat can provide essential amino acids and micronutrients for human growth, maintenance, and health. Scientists believe that incorporating meat in the human diet had a major role in human evolution. Researchers argue that as human gut capacity relative to body size is smaller and foraging cannot provide enough nutrients for their needs, considering lack of sufficient organs to consume high quality well-protected plant products such as nuts etc. consuming meat by early humans resulted in receiving these essential micronutrients and amino acids, and therefore over the years led to larger brain size relative to the body size (Milton, 1999).

Nowadays, there is an increasing global demand for high-quality protein products. Over the last century, world population has increased enormously. According to the most recent FAO statistics, the total world population has increased from 2.5 billion in 1950 to 7.5 billion in 2017 (FAO, 2017). This growth and rising income in the meantime in developing countries (which help those people to change their diet to consume more proteins and meat) are driving up global food demand. It has been reported in 2015 the world's meat consumption was 15.3 kg/capita pork, 13.8 kg/capita poultry, 10.1 kg/capita beef and 2.1 kg/capita lamb. In addition, it is projected that these amounts will increase to 15.1 kg/capita pork, 17.2 kg/capita poultry, 17 kg/capita beef and 2.4 kg/capita lamb in 2030. Beef is the third most commonly consumed meat all around the world. It is also estimated that the demand for beef meat, will be more than any other type of meat by 2030 (Statista, 2018). The marketing of beef in most countries is adjusted by observing criteria post slaughter and categorizing the quality of the meat. The point of classification is sometimes depending on the market's demand for particular attributes of the animal product.

The beef industry is an important section of the Canadian economy, with 3.83 million beef cattle population. This industry provides $17.2 billion to Canadian GDP (Gross Domestic Product) with 47% export of its annual production overseas, which places Canada sixth among the largest beef exporters in the world (Canadian Cattlemen's Association 2017). Therefore, the Canadian beef industry continuously endeavors for producing high quality meat.

Still Farm Credit Canada reported that beef consumption index (per capita) in past 15 years has declined. Despite the fact that the demand index for acceptable quality beef is still increasing and consumers are willing to pay more for a good quality product. This shows that there is a gap between beef quality products in the market and what is expected by the consumers (Sobool, 2015). Moreover, the most recent Canadian national beef quality audit showed that overall satisfaction of meat quality is determined by tenderness, juiciness and flavor. This study also stated that main quality concern for consumers is texture which per se is a combination of tenderness and juiciness (Beef Cattle Research Council, 2018).

The main purpose of beef cattle breeding around the world is to produce a high quality and uniform meat in an economically sustainable procedure to meet the consumer's demand. Despite its importance there are some challenges facing the industry such as feed costs and inconsistent meat quality (Beef Cattle Research Council, 2018). Beef quality in general includes all criteria which are essential for its consumption. These aspects include safety, nutritional value, palatability attributes and appearance (color) of the meat. Improvements in meat quality and palatability attributes will benefit both consumers and producers (Mateescu, Garrick, and Reecy 2017). Meat quality is a concept which is difficult to define and is controlled by many constituent traits. While other factors such as safety and nutritional value are of importance, sensory attributes play major roles in consumer acceptability and purchase decision of meat. Among others, these attributes include tenderness, juiciness, flavor, and the level of intramuscular fat. The most imperative factor in meat palatability is tenderness (Leal-Gutiérrez et al., 2018; Miller, Carr, Ramsey, Crockett, & Hoover, 2001; Smith, Culp, & Carpenter, 1974). In fact, consumers choose their household meats based on the sensory considerations. Especially they have shown a strong willingness to pay a premium for "tender meat" (Lee et al., 2014).

As consumers are willing to pay more for better meat quality, and to maximize gained revenue per each animal, it is important to focus on the procedures that will result in better meat-eating quality driving sustainability of the beef industry while meeting consumer demand in the meantime.

1.2 Beef meat quality

There are elements that are pivotal for the quality of meat. These elements include safety, nutritional value of the meat and palatability attributes (including tenderness, juiciness, flavor) as well as the appearance of the meat specifically color which affects consumer's perception of the product.

1.2.1. Safety and nutritional value

The annotation for food safety is the assurance for the customer to not be harmed during preparation and eating of the food (FAO/WHO, 1997). The pathogens and their toxins, which are the main cause of problems in consuming animal products, are present in the beef production chain from farm to food industry. Over the past years, meat producers and the industry tried to improve the food safety for consumers. For this aim, the industry took advantage of up-to-date advancements and protocols to reduce the pathogens and thereby produce safer outputs for customers. There are several important factors for the safety of beef meat. At first, the focus is on the harvest floor to prevent the product's contamination by external and internal elements such as environmental or gastrointestinal pathogens contamination. Also, there are other actions that need to be taken into consideration to prevent these hazards from occurring such as controlling the farm and feed yard condition, where is a good place to start pathogen control (Brashears & Chaves, 2017).

Nutrition value of the meat is one of the most important part in human diets because of its ingredients. The meat components are essential for maintaining human health and necessary for having a well-balanced diet. It contains proteins with high biological value, essential amino acids, energy, fatty acids, and a variety range of vitamins and minerals. Biological value of proteins is how we determine the efficiency of body in utilizing consumed proteins in the diet. High biological values are correlated with high amounts of essential amino acids. (Hoffman & Falvo, 2004).

Muscles are generally classified as red, white or intermediate. Red meat originates from beef, goat, sheep, veal, and pork. Meat composition and the nutritional values are different and depends on the animal. Proteins in the meat have high biological value. It has been shown that there are eight amino acids that the human body is unable to produce (essential amino acids) which are present in all muscle foods, and red meat such as beef and lamb contains all of them (Purchas, Wilkinson, Carruthers, & Jackson, 2014). Additionally, beef is a rich source of the vitamins Niacin (B3), Pyridoxine (B12), and Cobalamin (B12). It also contains other types of vitamins in lower amounts such as Retinol (A), Ascorbic Acid (C), cholecalciferol (D) and α-tocopherol (E). As well as potassium, iron, phosphorus and zinc with the lower amounts of magnesium, calcium, and copper and a useful amount of selenium. Lastly, fatty acid composition is the other factor that affects the nutritional value. They are present in adipose (fat) tissue in triacylglycerol form, which is called neutral lipid (NL), and in addition in marbled muscle. Furthermore, they are present in the muscle cell membrane in phospholipid form (PL). The NL and PL fatty acids are present in three types: SFA (saturated fatty acids, without double bond, all single bonds in the fatty acid chain), MUFA (monounsaturated fatty acids, with one double bond), and PUFA (polyunsaturated fatty acid, with more than one double bond in the fatty acid chain). In NL fatty acids, there is a higher percentage of SFA and MUFA types and they can be synthesized in the body, commonly in adipose tissue. On the other hand, PL fatty acids have higher percentages of PUFA and food can provide these nutrients. The muscle of beef has higher levels of SFA and lower content of PUFA. The main dietary PUFA are linoleic acid (LA) and α-linoleic acid (ALA) which the human body is not able to produce while they have a major role in metabolism. These fatty acids are present in plants and when animals consume the plants, they receive them. While LA and ALA both go through degradation in the cattle rumen during the digestion process and only a low level of them remains unchanged, however, with high levels of foraging in beef cattle rearing the level of both fatty acids in beef muscle will be relatively high.

This is important in human diet fortification and helpful for creating a balanced diet and thus impact the marketing of the beef meat at the marketplace as nowadays the majority of people are shifting their food choices towards healthier options. (Wood 2017, Food Standards Agency 2002).

1.2.2. Colour attributes

One of the most important facts that impacts consumer's choice at point of purchase of a meat product is the appearance of the meat specifically, color. Consumers consider discolored meat as a sign of spoiled product which affects their choice of purchase. Almost 15% of retailed beef and corresponding $1 billion annual revenue loss is due to discounts because of meat discolorations (Smith, Belk, Sofos, Tatum, & Williams, 2000).While meat is a nutritious part of a human diet, customers do not show a willingness to buy a product, which does not appear as expected in terms of color consistency. Normally, consumers consider bright red color as an indicator of fresh beef and, any other color such as brownish as unexpected color. Thus, other colors are less appealing and will affect consumer's choice of purchasing and re-purchasing a product. The reason behind it might be the fact that spoiled meat has the same range of color and these unexpected colors associates with spoilage in consumer's mind (Suman & Joseph, 2013).

The color is a combination of physical and chemical attributes. Some factors can affect the meat's color such as the level of moisture in the meat, the myoglobin protein (which is a type of iron carrying macromolecule), its concentration, and stability. Level of surface moisture in the meat implies the degree of light that is reflected to customer's eyes and it affects their choice (Faustman & Suman, 2017). Myoglobin protein plays a pivotal role in meat color hence the interaction between these molecules with others in tissue matrix will not stop after slaughter, post-mortem aging, and processing as there is still energy and oxygen available in the muscle. Many factors can affect myoglobin concentration, and hence color of the meat. These factors include species, breed, sex, muscle type, age of the animal as well as genetics. Researchers reported that myoglobin content in beef is greatly impacted by genetics and particularly the cattle breed (King, Shackelford, Rodriguez, & Wheeler, 2011; Matarneh, England, Scheffler, & Gerrard, 2017).

The concentration of myoglobin proteins is different and depends on the type of muscle. For example, the "red muscle" (such as dark meat) that have a considerable amount of slow twitch myofibers, have higher levels of myoglobin protein. Whereas the "white muscle" has more fast-twitch fibers and lower levels of these proteins. The higher the concentration of myoglobin the color will be more intense (Matarneh et al., 2017). The structure of myoglobin is important and can affect the color in the meat. Myoglobin is a combination of an apoprotein, and heme and it contains 153 amino acids. The heme, which is a part of this molecule, is responsible for the red color in the fresh meat. After slaughter and post-mortem the heme chemistry remains active, and as a result, the raw meat appears red in color. The type of iron in myoglobin, which is present in fresh meat, is a ferrous non-oxygenated form which results in purple-red color. With cutting the meat and its exposure to oxygen in the air it will change to ferrous red oxymyoglobin, this process is called "blooming" and that has an effect on meat's color which can be perceived as fresh by consumers. As time passes by eventually the heme iron in oxymyoglobin will be oxidized to ferric state to metmyoglobin. This is the result of disconnection of oxygen with iron and its binding with water. In this state the color of the meat will appear brown (Faustman & Suman, 2017).

1.2.3. Palatability attributes

Beef palatability attributes are determined by different factors, including tenderness, juiciness, and flavor (Miller et al., 2001). These attributes are very important for consumer satisfaction and choice for purchasing and re-purchasing a product. The major source of dissatisfaction in consuming beef originates from these attributes. A recent beef quality audit across Canada showed that major quality concern in beef consumption stems from inconsistency in these attributes specifically tenderness, juiciness and flavor (Beef Cattle Research Council, 2018).

This lack in consistency in quality attributes in meat originates from heterogeneous muscles combination in beef cuts. There is a considerable difference between muscles in traditional beef cuts regarding its texture and histological characteristics (Paul, Mandigo, & Arthaud, 1970). Early studies showed that beef muscles vary in many aspects including pH, size, weight, composition and ultrastructure (Ramsbottom & Strandine, 1948; Strandine, Koonz, & Ramsbottom, 1949). These early studies also showed that meat tenderness, palatability, juiciness and flavor intensity differ between various muscles (Carmack et al 1995; Johnson et al., 1988; Ramsbottom, Strandine, & Koonz, 1945). It has been reported that different muscles will respond differently to post-mortem aging period (Koohmaraie et al., 1988).

Traditionally loin and rib primal of beef whole muscle retail for steaks since they have relatively better amounts of desired palatability attributes such as tenderness, flavor and juiciness. Comparing to rib and loin, chunk and round steaks are less used as they have lower quality attributes and thus they commonly used as ground or low quality steaks or roasts (Nyquist et al., 2018). Calkins & Sullivan (2007) published a paper about ranking of different muscles in beef according to their WBSF score in addition to sensory tenderness, flavor and juiciness. They stated that Longissimus muscle is ranked as intermediate to tough. This muscle is located in ribeye and loineye (Longissimus in the chuck) and marketed as a premium cut, thus it is important to improve tenderness and consistency of meat palatability attributes in it.

1.2.3.1. Tenderness

Considering consumer's perspective, tenderness is the most important factor affecting meat palatability. In general, the genetic makeup, breeding condition, slaughter and post-mortem aging, and at last processing in the food industry have significant effects on meat tenderness (Leal-Gutiérrez & Mateescu, 2019). Because of the vast number of contributing factors, it is hard to control meat tenderness entirely and so this may result in an inconsistent product, which will bring dissatisfaction for consumers and at the end will negatively impact the beef industry. Tenderness in beef cattle per se depends upon the level of connective tissue, the muscle structure, level of intramuscular fat content and myofibrillar protein degradation known as biochemical attributes after slaughter (Picard & Gagaoua, 2017). Here we briefly look into these elements.

1.2.3.1.1. Macroscopic scale of muscle structure

Skeletal muscles consist of muscle fibers, connective and fat tissue. The muscle fibers include cellular components (i.e. cell membrane, enzymes, myoglobin, and myofibrils). In a macroscopic scale, there are several parts in a muscle tissue. Connective tissue by itself has three parts: Endomysium (the layer that encircles each muscle fiber), Perimysium (which covers the bundles of muscle fibers), and Epimysium (the layer that encloses the muscle as a whole). In addition, skeletal muscle consists of fat, vascular, and nervous tissues, which are important in its function (Listrat et al., 2015) (Figure 1.1).

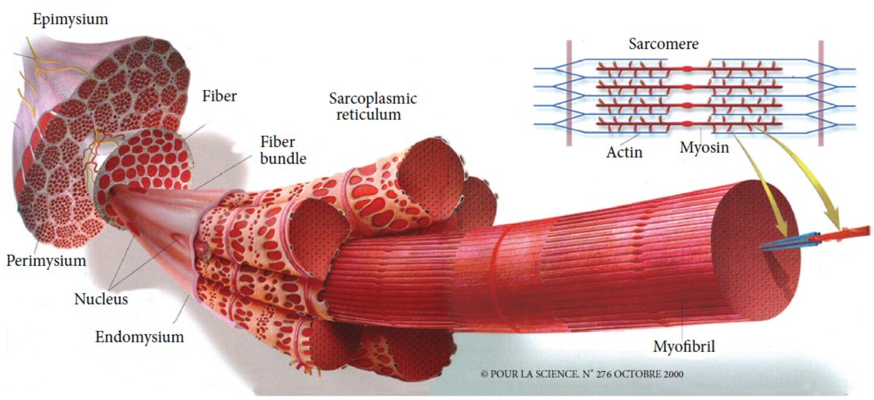

Figure 1. 1 Macroscopic view of the muscle. (image from Listrat et al. 2015)

1.2.3.1.2. The microscopic scale of muscle structure

At the microscopic scale, the muscle fibers are stretched cells with multiple nuclei. Their shape is like a spindle. The length of these cells varies and depends on the type of animal, from some millimeters to several centimeters. The plasma membrane of muscle fibers called "Sarcolemma" which has cross-sectional areas (CSA) and their role is in muscle metabolism and contraction.

In general, myofibrils are joined up together in bundles with a diameter around one micrometer. These bundles have subsections made up of myofilaments. With electron microscopy observation of longitudinal cross from myofibrils, different parts are known. These include the "A" band (dark parts) and "I" band (light sections). The "I" bands are separated in two parts by a "Z" line. In addition, there is a repeating unit between two Z lines which is Sarcomere (acting as the contractile unit of myofibrils). The myofilaments are in two types, thin and thick. The thin myofilaments are built up from the proteins actin, troponins T, I, and C (which have a regulatory role in contraction) and tropomyosin. They are arranged end to end and side by side with the actin filament. The thick myofilaments include myosin clusters, which have ATPase activity, and it provides energy for the muscle contraction by breaking down the ATP to ADP. The Sarcoplasm, which is the cytoplasm of muscle cells, have many soluble proteins like enzymes, and other elements such as glycogen and lipid droplets (Listrat et al., 2015) (Figure 1.2).

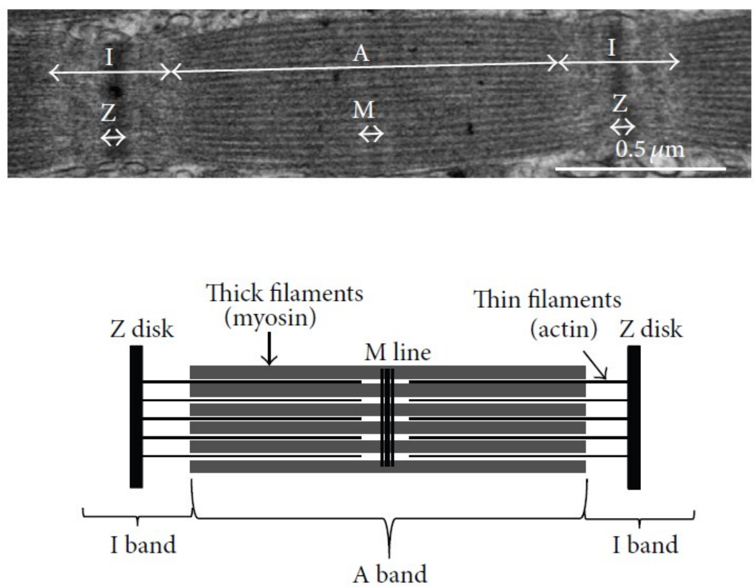

Figure 1. 2 The microscopic view of muscle filaments. (taken from Listrat et al. 2015)

Muscle contraction in live animals happens when thick and thin filaments (which contain myosin and actin proteins respectively) in sarcomere slide together. The energy for the sliding process and thus muscle contractions as well as muscle relaxation comes from hydrolysis of ATP molecules. These contractions help the live animal with muscle movements. When the animal dies and there is no more ATP restoration process, the association between thick and thin filaments becomes permanently fixed and that is when rigor stage happens. Afterwards with different processes happening in the muscle, we could see the transition from muscle to meat (Astruc, 2014). Later on in this chapter we will see how these process will work and effect meat tenderness.

1.2.3.1.3. Connective tissue

The connective tissue in the muscle is composed of cells and extracellular matrix (ECM). The ECM is built of collagen fibers and it is wrapped by a matrix of proteoglycans (PGs). Collagen (which is from a fibrous protein family and is unfavorable for tenderness) have different types in mammals, and the major ones are fibrillar collagen type I and III. The amount of collagen in the tissue depends on the type of muscle, sex, genotype, species, and age. Nevertheless, a range of 1 to 15 percent of muscle dry weight in adult cattle is reported. The PGs that are present in connective tissues are complex and large molecules with a weight range from 40 to 350 kDa. These molecules can connect to other PGs and fibrous proteins like collagen. It has been shown that the PGs have small amounts in the muscle, ranges from 0.05 to 0.5 percent in adult cattle, per muscle dry weight**.** As much as the level of connective tissues in muscle increase, the toughness of the meat will rise (Listrat et al., 2015; Myllyharju, 2005)**.**

1.2.3.1.4. Intramuscular fat content

Intramuscular fat (IMF) is the amount of fat within muscles. In a chemical perspective, IMF includes phospholipids (mostly from cell membrane), triglycerides, and cholesterol. Marbling refers to the level of the white layer of IMF between the muscle's bundles. It is believed that the level of IMF has a positive effect on beef palatability traits such as juiciness and tenderness. Marbling is an important factor in beef meat grading, because of the willingness of customers in the market for paying more for guaranteed quality. As research showed that lower level of IMF and marbling will result in more dry meat, which from a customer perspective equates to less tasty (Hocquette et al. 2010).

1.2.3.1.5. Post-mortem aging

Post-mortem aging is a method for improving beef palatability attributes with storing it properly (Kahraman & Gürbüz, 2018). The storage of the meat should be in cold temperatures and for specific periods of time, days or weeks, for endogenous enzymes to work in order to enhance and develop palatability attributes such as tenderness, flavor and juiciness through muscle sarcomere breakdown. Different studies suggest that with increasing length of aging, palatability attributes are enhanced (Khan et al., 2016). These developments were extensively studied and attributed to endogenous enzyme activity present in the muscle. Of some of major enzymes involved in myofibrillar degradation process post-mortem resulting in tenderness improvement we can mention µ-calpain, m-calpain, which are calcium dependent as well as Calpastatin as their inhibitor. In addition, carbohydrate, fat and other precursors such as ribonucleotides (after hydrolysis) play a major role in flavor enhancement. Carbohydrates would break down to sugars, fats will be converted to fatty acids and ribonucleotides to inositol or guanidine monophosphate (IMP/GMP), (Koutsidis et al. 2008; Aaslyng and Meinert 2017; Khan et al. 2016).

In general, post-mortem aging of the meat takes place in two different forms, dry and wet. Both of these methods will result in a quality enhancement for the product, but the process and conditions leading to the final product differs. Post-mortem dry aging is one of the oldest methods in which large pieces of meat would be hung in a cooler or cold storage room without being packaged for a period of time. Conversely, for wet aging post-mortem, pieces of meat would be vacuum packaged in specific impermeable bags and kept in a cooler for a period of time (Kahraman and Gürbüz 2018; Khan et al. 2016).

Wet post-mortem aging of the beef is an economically valuable method as the wet packaged beef is suitable for transporting the product as well as enlarging the product yield. Higher product yield will be achieved through decreasing product loss due to evaporation and excess trimming compared to a dry aging process. Studies reported that with wet aging metallic and bloody flavor are developed as opposed to dry aging method which results in a more beefy or roast properties flavor wise. This could be due to different levels of precursors concentration as dry aged beef has lost its own moisture (Khan et al. 2016). Because of this, dry aged meat has higher price in the market (Khan et al. 2016; Dashdorj et al. 2016). For proper meat dry post-mortem aging, some essential standardized protocols should be considered. These conditions include proper temperature in storage area (from 0 to 3 or 4 ^{o}C and not lower than -2^{o}C), humidity (between 61-85% of relative humidity), sufficient air velocity (0.2-0.5 m/s or as some studies suggest 0.5-2 m/s) and adequate period of time for achieving proper product (Dashdorj et al., 2016; Kahraman & Gürbüz, 2018).

With post-mortem aging as it has been mentioned before, some biochemical changes happen in the meat which results in a product with higher palatability attributes. Here we briefly look into these changes.

1.2.3.1.6. Myofibrillar protein degradation and turnover

As it has been mentioned, most of the skeletal muscle is myofibrillar protein and its state (biochemical attributes) is directly related to meat tenderness. The turnover of myofibrillar proteins is complicated and yet unknown. Nevertheless, the best model that is presented up to now claims that for having a functional muscle, the process should happen at the myofibril cell surface, starting with disassembly of myofibrils to myofilaments and then they will go through a degradation phase, which produces polypeptides and finally amino acids. These changes happen by important key factors like protease enzymes, the calpain system, proteasome, and the lysosomal proteolysis. Among all, the most predominant factor is the calpain system that has a specific proteolytic role in releasing myofilaments which will result in more tender meat at the final step (Koohmaraie, 2002).

Proteases are enzymes with cleavage activity on proteins and peptides. They are specifically designed to breakdown particular sites of protein sequences. Cysteine proteases known as thiol proteases which have a big super family that share a common catalytic process that includes a nucleophilic cysteine thiol. Cysteine proteases are commonly found in fruits such as pineapple, kiwi and papaya and they can be used for tenderizing the meat. Up to now, researchers found 14 members of the super family for cysteine proteases, and each family is differentiated by the site of catalytic triad on the protein [catalytic triad is the active site of the enzyme containing three amino acids which can be found in hydrolyze or transference enzymes]. Calpain and cathepsin enzymes are categorized in the CA clan in cysteine proteases superfamily (Buttle & Mort, 2004; Moldoveanu, Hosfield, Lim, Jia, & Davies, 2003). In the muscle we can see both cysteine protease enzymes and their inhibitors which are called “Cystatins” and they are distributed throughout muscle cells. Cystatins can modulate the activity of the cysteine proteases. So, in post-mortem as the pH is in favor of many cathepsins, we expect to see a lot of protein degradation especially of myosin and actin part. However, because of cystatin activity, cathepsins will be inhibited and will have very low activity post-mortem, in normal storage condition and in the first week after slaughter (which is the time that the most part of tenderization happens). But if we keep the meat for longer period of time and in higher temperatures, we would have more tender meat. As the cathepsins activity is limited post-mortem, research has focused on the calpain system in the muscle, which is active post-mortem and degrades muscle proteins in normal storage condition and with its activity, by degrading the proteins into shorter fragments and tenderize the meat (Hopkins & Huff-Lonergan, 2004).

Calpain is a calcium-activated neutral cysteine proteinase that has several family members, in charge of taking care of several duties inside the cell, including pivotal cellular activities like cell motility, cell proliferation, and apoptosis. Up to now, more than 14 calpain family members in different tissues of mammals have been recognized and they are considered as conserved non-lysosomal cysteine proteases. They have a molecular weight between 30 kDa to 80kDa and it varies depending on their function inside the cell (Storr, Carragher, Frame, Parr, & Martin, 2011). The isoforms of the calpain family are different in their N-terminal sequences, their regulatory structure and calcium binding site. Researchers with regard to their structure, classified them into five domains. The first one is short amino acids domain (19 amino acids) in N-terminal part which separate during the auto-proteolysis. The second domain that is catalytic domain have two subparts (IIa and IIb) and the active site is the origin of the gap between these two parts. The third domain is the regulatory site which has attenuative phosphorylation and a possible phospholipid connection part. The last domain includes five parts which can bind with calcium. The µCalpain and mCalpain are two types of ubiquitous isoforms which have been found to have an effective role in wound motility, immune responses to tumor, apoptosis and protein degradation in muscular tissues. These two isoforms are named after their relative response to calcium concentration, whereas µCalpain and mCalpain respond to micromolar and millimolar calcium levels respectively in the environment (Wells & Leloup, 2010).

1.2.3.1.7. Calpain relationship to muscle growth and post-mortem tenderness

Bioactive proteins, called enzymes, are important in muscle development. Muscle mass is defined by two items, Hyperplasia and Hypertrophy, which are increase in cell number and size respectively. Where the cell number is controlled by proliferation process and size is related to the balance between synthesized and degraded protein (Koohmaraie, 2002). Previous studies indicated that calpain isoforms (considered as endogenous enzymes) play key roles in muscle myogenesis, myoblast migration and also fusion into myotubes and based on mouse model experiments it is clear that lack of calpain isoform activities may result in muscle dystrophy (Wells and Leloup, 2010). Although calpain isoforms have major roles in muscle development, after death there is a series of reactions in muscle tissue which result in more tender meat. After death, some of endogenous enzymes stop working while a few are still active in the muscle and work throughout all the post-mortem aging period. Two of the most important active enzymes in this period are the calpain family and cathepsins. Studies showed that after death, µCalpain, which is sensitive to micromolar concentrations of calcium (3 and 50 µmol l-1 calcium for half-maximal activity), are still significantly active and working on a number of proteins making up the myofibrils such as titin, nebulin, desmin, tropomyosin, troponin-T and c-protein. The optimal pH for Calpain family is 7 to 7.2 but it should be mentioned that they will be still significantly active at pH equal to 5.5 to 5.6 after death (this decrease in the pH from 7.2 to 5.5 is the output of lactic acid synthesis in lack of oxygen) (Hopkins & Huff-Lonergan, 2004; Xiong, 2017).

Although Ca^{2+} is required for the µCalpain and mCalpain activity, in post-mortem aging, when µCalpain and mCalpain are incubated with calcium, they autolyze (self-degrade) and this will result in reduced mass in their structure and thereby they will need less calcium for their half maximal activity. However, when this autolysis continues the enzyme will be deactivated finally.

Also, studies showed that both autolyzed and non-autolyzed forms of these enzymes have activity (Hopkins & Huff-Lonergan, 2004). In addition, Cathepsins are in the acidic group of proteases, normally present in lysosomes. There is a belief that they are working on collagen degradation and they can degrade the same substrates of Calpains plus myosin and actin in lower pH (3.5-4.5). Despite the above-mentioned items for Cathepsins, because of several reasons scientists think that they do not have an effective role in meat tenderizing. First, the lysosomal membrane per se which prevent the direct contact between cathepsins and myofibrils. Second, they need very low pH for activity (pH 1-2) and finally some results showed that after aging for two weeks there is no significant change in myosin and actin content which are potentially the Cathepsin substrates (Xiong, 2017).

1.2.3.1.8. Calpain and Calpastatin system

Calpastatin is the inhibitor of calcium dependent enzymes like Calpain family. Previous research showed that the relation between Calpain and Calpastatin is pivotal for muscle to keep itself in a normal condition. Increased muscle mass can be a result of reduction in muscle protein degradation which is per se originated from inhibitory effect of Calpastatin on Calpain family (especially µCalpain and mCalpain) in the muscle tissue (Juszczuk-Kubiak, Wyszyńska-Koko, Wicińska, & Rosochacki, 2008). Calpastatin is an exceptional inhibitor with a multiheaded structure. Four of its five domains (I, II, III, IV) are similar to each other to some extent, they include 140 amino acids with inhibitory activity, the last domain (L domain) is a N-terminal part which does not have inhibitory action. Each of those four inhibitory domains are able to control one Calpain, as a result Calpastatin has a strong inhibitory behavior on calpain molecules (Wendt, Thompson, & Goll, 2004). Studies showed that the level of inhibitory activity of

Calpastatin will drop by time in the post-mortem aging period. In addition, the level of Calpastatin in the muscle at 24 hours after slaughter has correlation with tenderness of the meat, as Calpastatin degrades by time in post-mortem aging, the rate of its degradation has a positive effect on calpain proteolysis enzyme family. This means that with its degradation, its ability to inhibit calpain enzymes will reduced and so those enzymes can continue to their activity in the meat. Even though there has been a lot of research on this regulation, still some facts are unknown (Hopkins & Huff-Lonergan, 2004). Thus, the presence of Calpastatin postmortem is not a positive occurrence because it will extend the aging process to reach the optimum tenderness.

Calpains are encoded by *CAPN1* gene and Calpastatin as its inhibitor is encoded by *CAST* genes in the genome (Koohmaraie, 1996). The proteolytic system between these two enzymes is reported to be related to palatability attributes in beef meat (Bolormaa et al., 2014; Leal-Gutiérrez et al., 2018). Several markers regarding *CAST* and *CAPN1* genes have been identified in different studies (Allais et al., 2011; Casas et al., 2006; Page et al., 2002; Pinto et al., 2010; Van Eenennaam et al., 2007). These studies also showed that there is a genetic association between meat tenderness and individual markers related to these genes. Different markers are reported for *CAPN1* gene. Some of these markers related to calpain and Calpastatin genes are briefly reviewed here.

Between markers reported for Calpain gene, firstly we can mention Capn4751 which has a polymorphism located in intron 18 of *calpain*. It has been reported that this marker is associated with tenderness in beef at days 7, 14 and 21 of post-mortem aging (Pinto et al., 2010). Next marker identified named Capn316 which is located in exon 9 of *calpain* (Allais et al., 2011). It has been reported that this marker is associated with shear force at days 7, 14 and 21 of post-mortem aging in beef (Pinto et al., 2010). Last marker worth mentioning is named Capn530 which is located in exon 14 of *calpain* (Allais et al., 2011). This marker also is reported to be related to shear force at day 14 of post-mortem aging in beef cattle (Page et al., 2002).

Among markers identified for *Calpastatin*, UoG-Cast and WsuCast is SNP located at intron 5 of *CAST* gene (Van Eenennaam et al., 2007). Studies reported that this marker is related to tenderness in beef (Allais et al., 2011; Van Eenennaam et al., 2007). Cast2959 is another marker which is located in the 3′UTR of the *Calpastatin* mRNA. It has been reported this marker is associated with tenderness and shear force in beef (Casas et al., 2006). Lastly, Cast2832 is a marker located in the 3′UTR position of the *CAST* mRNA which has been reported to be related to shear force in beef (Leal-Gutiérrez et al., 2018). Cast2959 and Cast2832 in Angus–Brahman crossbred and Brahman population reported to have lower transcription in specific genotypes which means less Calpastatin protein production and thus less inhibition on μ-calpain during post-mortem aging (Leal-Gutiérrez et al., 2018; Nattrass et al., 2014).

These biological markers related to Calpain and Calpastatin system can be useful for meat quality prediction using genomic and transcriptomics approaches (Hocquette et al., 2012). Using these approaches, we can identify markers related to meat palatability traits in live animals for both selective breeding programs to improve these traits for next generations, and useful for individual animal management thus each animal could meet its potential.

1.2.3.2. Water holding capacity and juiciness

Water holding capacity (WHC) is one of the aspects that influence customer’s decision when buying meat and its related products. WHC can be determined by levels of reduction in water concentration in a product during different stages such as transportation, aging and storage, processing and finally cooking. In other words, water-holding capacity is the level of bound water in the raw meat in addition to the amount of water that is added to meat in different processing stages. Wood (2017) reported that the average amount of water in different beef meat cuts is around 70-75%, and protein content is between 20-22%, fat content around 4% and the rest is carbohydrates and minerals. The amount of tissue lipid may vary depending on different factors which can directly influence the WHC (Warner 2017). Juiciness definition is the level of moisture (which is related to the wetness of the meat and thereby the WHC) and lubrication (which is related to the level of fat content that stimulate saliva flow) of meat when it is chewed by the user. Because juiciness is a sensory trait, it is defined by either customers or a trained sensory panel to grade meat products. In customer grading manner, up to 10% variation in overall acceptability will be considered for grading a juicy meat (Hui et al. 2012; Warner 2017).

1.2.3.3. Flavor

Regarding eating quality of meat, one of the important factors is its flavor, which is described as the taste of a meat in combination with its smell, and these two items propose a unique sense for meat users. There are distinct and vast numbers of factors that have a considerable impact on meat's flavor, both pre- and post-slaughter. For instance, the breed and genetic makeup, age, sex, diet, stress, fat level and its structure and content stand for pre-slaughter contributing factors while slaughter process, handling, aging, storage and cooking methods are important as post-slaughter elements (Khan, Jo, and Tariq 2015; Dagne and Negassi 2017). Mammals have receptors for basic tastes, including bitter, salty, sweet, sour and umami. The meat's flavor comes from its precursors mainly from amino acids and peptide content. It has been shown that the sweet taste in meat is related to L amino acids such as Ser, Gln, Gly, Thr, Ala, Val, Met, Lys, Pro, Cys while the sour taste comes from Thr, Asp, Glu, Asn, and finally, the bitter taste referred to hydrophobic amino acids including Tyr, Val, Met, Trp, Phe, Ile, Leu, His, Arg, Lys, Pro, Cys. On the other hand, the umami taste per se mainly originates from glutamate, and other molecules such as L-glutamic acid and its monosodium salt, L aspartic acid, succinic acid, tartaric acid, 5′-ribonucleotides and several pyro-glutamate peptides. In addition, during cooking, the heat contributes to changes in the meat biological elements. For example, degradation of vitamin B1 (thiamin) glycogen, sugars, and organic acids. Altogether, the cooking process plays a major role in the final flavor of meat (Flores, 2017).

One of the important contributors in flavor formation in cooked meat is a chemical reaction happening during cooking between reducing sugars present in the meat and amino acids as well as lipids called "Maillard reaction". In cooking procedure Maillard reaction is responsible for flavor compound formation. During cooking of the meat fat component will provide species specific flavor while lean provides the known meaty flavor in all meat products (Mottram, 1998; Nursten, 2002).

1.2.4. Methods in evaluating beef palatability attributes

Palatability attributes of the meat are important, and they can affect a consumer's perspective of a product. In order to measure palatability and quality attributes of the beef meat we can use objective and subjective methods. Basically, objective oriented measurements are applied by using specific protocols and instruments followed by data collection. On the other hand, in a subjective measurement, a group of people will rate a product in respect to its properties.

One of the most important palatability traits is tenderness of the meat (Leal-Gutiérrez & Mateescu, 2019). In the first impression, it may look that meat's tenderness can be simply determined as the necessary force in biting a piece of meat, however, this thought is the base behind many mechanical instruments that measure the force of cutting the meat, still even the most precise measures only account for near 60 percent of tenderness variation when trained sensory panel evaluate. This might be because of the fact that consumer's acceptability of meat is influenced by many factors not only the biting force (Purchas, 2014).

Tenderness can be measured in two different ways objectively and subjectively. For objective measurements laboratory instruments are used to access toughness of a piece of meat using the force for cutting through it. For this purpose, a common method is evaluating by Warner-Bratzler shear force (WBSF) which measures the amount of shear force (kg or Newtons) that is necessary to cut through a specific piece of meat (i.e. *Longissimus dorsi* muscle in cattle) that is trimmed and cooked. It is important to have a standard blade in a standard procedure cutting through a round piece of meat, shearing across the meat fibers as well as recording the used force (Destefanis, Brugiapaglia, Barge, & Dal Molin, 2008; Silva et al., 2015). Solomon et al. (2010) reported the relationship between WBSF and panel scoring is moderate to strong (R ranges from 0.63 to 0.92). For WBSF measurements, a standard blade is used to shear through a cooked sample parallel to fiber grain of the meat with a specified speed and a machine will record the force used to cut through it (AMSA, 2016).

In addition to WBSF, tenderness can be evaluated subjectively and with a trained sensory panel assessment or consumer panel ratings to understand the level of acceptability of a product (Caine, Aalhus, Best, Dugan, & Jeremiah, 2003; Sitz, Calkins, Feuz, Umberge, & Eskridge, 2005). Sensory measurements are very important as objective methods are not capable of assessing the quality of a product as a person's experience through eating a product (Bruce & Aalhus, 2017a). In 2016, Amerincan Meat Science Association (AMSA, 2016) published a second edition of guidelines for different measurements of tenderness including sensory attributes. Sensory measurements are explained as a degree of difference that attributes of a meat sample can be tested to understand the descriptive properties of that product. For trained sensory panel analysis, a group of people would be trained to understand and accurately assess palatability attributes of standard prepared samples according to the guidelines. While for consumer panel ratings, a large number of consumers rate a product and highlight particular desirable and unfavorable attributes of a product. Consumer assessments and ratings are not appropriate for extensive product characterization and for this purpose a trained panel is advised (Bruce & Aalhus, 2017a).

Other types of objective measurements include meat pH, and color indices (lightness, Hue and Chroma). pH of the meat is important after slaughter and during post-mortem aging period changes and per se affects meat quality attributes. After slaughter, due to anaerobic glycolysis in the muscle, hydrogen ions concentration increases which results in drop of pH of the meat (Bendall, 1973). This would result in decrease of pH from 7.2 to 5.6 in post-mortem aging. This drop in pH affects meat palatability and quality (Matarneh et al. 2017). With decline in pH of the meat, muscle proteins will achieve net charge of zero in which the pH is at isoelectric point of the proteins in the muscle. With this zero-net charge proteins that are present in the muscle will attract together, resulting in decrease of space and thus reduction of available water holding capacity in the muscle. In addition to that, electrostatic repulsion in the muscle will be reduced or eradicated resulting in tightening of myofilaments in the muscle together and hence purge loss of the meat (Matarneh et al. 2017). Normal ultimate pH range can be between 5.5-5.8 which helps in improving quality attributes in meat, while lower pH (<5.5) or higher pH (>5.8) will result is pale soft exudative (in pork), and dark cutting meat (in beef), respectively (Tarrant, 1989;

Wismer-Pedersen, 1959). Changes in the meat pH, the rate and its extent also affects meat color. As pH affects the spacing of muscle fibers by changing the protein charges, which results in light reflectance and absorbance on surface of the meat, hence color changes of the product can be observed (Boles & Pegg, 2005). Color changes can be measured objectively. Commission Internationale de l'Eclairage (CIE) in 1931 suggested to collect three dimensional values (XYZ) for accurate color assessment, including L*, a* and b* for color measurements. These indices cover brightness of the meat (L*), and color of the meat (−a: green to +a: red, and −b: blue to +b: yellow). These indices then can be converted to lightness, Hue (color of the meat itself) and Chroma (saturation index) for better understanding meat color (AMSA 2016).

1.2.5. Previous studies on heritability and genetic correlation estimates and prediction approaches for meat quality attributes

Similar to production traits, there is possibility to improve meat quality and palatability attributes through genetic selection. Heritability and genetic parameter estimation for these traits helps as a starting point of designing breeding plans (Gill et al., 2010a). Although practically, due to low to moderate heritability estimates for these traits (values ranging from 0.1 to 0.3) in beef cattle, their difficulty of measurement as well as being time consuming and expensive, are not easy to be incorporated as selection criteria (Warner et al. 2010). On the other hand, there are some objective measurements suggested for meat quality attribute assessment such as WBSF and color measurements, but they are not completely explaining different aspects of eating quality (Warriss, 2000). These beef quality attributes are very important and have high economical value as they play an important role in consumer's acceptance and choice of the product in the market and thus on revenue per animal for farmers. Acquiring knowledge about these traits, such as variance component and heritability estimates, as well as phenotypic and genetic correlations will enable producers to overcome possible challenges such is inconsistency in meat palatability attributes, and help them for the development of further breeding programs (Leal-Gutiérrez & Mateescu, 2019).

Phenotypic correlations calculated in different ways as Pearson coefficient without considering individuals relationships (Statstutor, 2015) and/or considering the relationships between them (Cheverud, 1988) are important. These estimations help producers to have a better understand of consistency of the traits over time as well as their set relationship together over many generations. In addition to that, heritability estimates show how phenotype of the traits follows the genetic material of an animal considering variations that originated from genetic and environmental factors. Heritability and variance component estimates for a trait can indicate the ratio that is controlled by genes versus other factors and can be passed down to future generations in different populations (Visscher et al. 2008). Highly to moderately heritable traits indicates that the phenotype of the animal is a good indicator of its genetic merit. This will allow us to improve that trait through selective breeding programs and improve those traits genetically. It is important to highlight that, for economically important traits even low heritability estimates should be considered in breeding programs for genetic progress and improvement through generations (Cassel, 2009). Palatability and quality attributes are economically important in the beef industry. The National Canadian beef quality audit (Beef Cattle Research Council, 2018) reported that sensory attributes including tenderness, juiciness and texture are factors which affects consumer's acceptance of a product the most. Reports from Farm Credit Canada (Sobool, 2015) also showed that a gap between beef consumption and demand (per capita) remains over the last 15 years. Therefore, we can conclude a lack of these palatability attributes that are most important for consumers. Providing information such as heritability for these traits can be very helpful for better understanding the nature of these traits as well as useful for targeting them for selection in breeding programs. Considering these economically important attributes, another genetic parameter that needs to be estimated is the genetic correlations between traits. In the genome, a single gene might influence many traits, a phenomenon known as pleiotropic effect of the genes (Cheverud, 1988). With calculating genetic correlation between these traits we can understand how much and in which direction they are related together, especially negative genetic correlations between meat quality attributes. This would help to have knowledge of the genetic background affecting complex phenotypes (Cassell, 2009). Having all this information in hand for the economically important beef quality attributes and with focus on producing consistent product as well as genetically improving them through generations, producers can meet market demands and maximize their revenue per animal.

Previous studies also showed that meat quality attributes are polygenic and influenced by different factors including breed, age, sex (Gao et al. 2007). One of the largest effects on palatability attributes in beef meat is the breed composition. This is particularly due to human genetic selection for desired phenotypes on animals during the development of cattle breeds for different purposes (Leal-Gutiérrez & Mateescu, 2019).

Mateescu et al. (2017) and Gill et al. (2010) in studying Angus and Angus sired beef breeds reported that there are moderate to high heritability estimates for tenderness (0.33), marbling (0.4), WBSF (0.38) and juiciness (0.22) while reported low heritability for flavor (0.16). In addition, Mateescu et al. (2015) reported high heritability for fat content (0.38), connective tissue (0.25), moderate for WBSF (0.19), panel tenderness (0.18) and very low for juiciness (0.06) in Angus sired beef. Pratt et al. (2013) reported a high to moderate heritability for sustained tenderness (0.31) and WBSF (0.23), and low heritability estimates for sustained juiciness across 10 different beef breeds.

Other researchers reported heritability estimates on beef palatability attributes for WBSF (ranges between 0.29 to 0.4), tenderness (ranges between 0.22 to 0.4), juiciness (0.09) and flavor intensity (0.07) (Dikeman et al., 2005a; Wheeler, Cundiff, Shackelford, & Koohmaraie, 2001). In addition, in a review of nine studies on meat palatability attributes from different USA universities Hocquette et al. (2005) reported average heritability estimates for tenderness (0.24) and fat content (0.49), as well as juiciness (0.11) and flavor (0.09). Garrick and Ruvinsky (2014) in a review on beef palatability studies across different breeds reported average heritability between sensory attributes. They indicated average heritability for tenderness (0.25), juiciness (0.22), flavor desirability (0.32) and overall acceptability (0.27) were high to moderate while connective tissue (0.12) and flavor intensity (0.10) had lower estimates. In addition, they reported the range between objective measured traits including lipid content (0.47-0.54) as well as WBSF (0.25-0.28), Calpastatin activity (0.26-0.43) and color attributes (0.17-0.29 for lightness, 0.13-0.17 for redness and 0.11 for yellowness). Lambe and Simm (2014) estimated the heritability of color attributes across species. They reported high heritability estimates for myoglobin content and for lean color low to moderate heritability.

Other studies estimating heritability for retail color attributes in Chianina beef breed reported very low heritability for lightness, Hue and Chroma before and 48 hours after storage (Cecchi, Russo, Preziuso, & Cianci, 2004a). King et al. (2010) estimated heritability of beef retail color attributes in seven different breeds in the USA. Between retail color traits lightness had moderate heritability (0.24 and 0.4) at day 0 and 6 of display while Chroma had a very low heritability (0 and 0.13). These researchers also indicated that a* and b* indices had very low heritability estimates at day 0 and day 6 of retail display.

Overall, these studies indicated that between objective measured traits WBSF had moderate to high heritability estimates. Estimated heritability for color attributes showed lightness has a low to moderate heritability as well as Hue, Chroma, a* and b* indices. Panel assessed sensory attributes indicated that tenderness and overall acceptability have moderate to high heritability while reported values for juiciness varied between different studies. The reason for some differences between these heritability estimates could be the fact that these studies used different breeds, population size (which have different exclusive features such as allele frequency) and different post-mortem aging periods. This information is useful for improving meat quality attributes (i.e., WBSF, color, sensory tenderness and palatability) in beef cattle by selection for genetic improvement in next generations.

Phenotype of palatability attributes describes how trained sensory panel perceived and assessed a particular sample. Researchers reported that sensory panel assessment for palatability traits is consistent and thus is one of the best methods for understanding these complex traits (Gill et al., 2010a). Pearson phenotypic correlation coefficient shows the relation of the traits to each other ignoring the relationship between themselves (Statstutor, 2015). This is particularly important in this study as we are looking into two different post-mortem aging periods and the consistency of these traits through time. For this aim, Pearson phenotypic coefficients >0.6 are considered as strong, 0.4-0.59 as moderate and <0.4 as low correlations (Evans, 1996). Reports on Canada's beef carcasses indicated that there are strong to moderate negative correlations between WBSF and overall tenderness, connective tissue and overall palatability (Caine et al., 2003). Jeremiah et al. (2003) in a study on Canadian AA beef carcasses reported positive and strong correlation between fat content and juiciness, while they found weak correlations between connective tissue, overall tenderness, flavor intensity, and overall palatability with fat content. Different studies on crossbred beef cattle indicated that there are strong phenotypic correlations between overall tenderness with connective tissue and juiciness (Shackelford et al. 1995) and WBSF and tenderness as well as weak phenotype correlations between meat pH and tenderness (Chambaz, Scheeder, Kreuzer, & Dufey, 2003). In this study, using crossbred beef cattle for assessing the quality attributes of the meat, the final products of commercially used breeds and the results of genetic selection on these traits can be investigated.

Looking at Pearson phenotypic correlations between color indices and panel attributes, Wulf and Page (2000) stated that correlations between lightness with tenderness, flavor intensity and juiciness were moderate to low. They also showed that a* and b* indices have moderate to weak phenotypic correlations to tenderness, flavor intensity and juiciness. Other studies also reported weak correlations between lightness, Chroma and Hue with beef fiber separation as well as texture (Modika et al., 2015). Another study on multi-breed beef in USA by Wulf et al. (1997) reported weak correlations between color attributes (lightness, a* and b*) and sensory traits (tenderness, juiciness and flavor).

In general, different studies indicated that there are strong negative correlations between WBSF and panel tenderness, as well as moderate negative correlations between WBSF and connective tissue and overall palatability. Moderate phenotypic correlations between fat content and juiciness and moderate to low between color indices (lightness, Hue, Chroma, a*, b*) also has been reported. There are considerable differences between studies for other sensory attributes and these variations could originate from small sample size and breed differences. Still for some traits we can see the consistency of correlations between studies which indicates the relation between these attributes. This information can be used to understand the relationship between these traits as well as their changes and consistency over post-mortem aging period.

Although Pearson's correlation coefficient is useful for understanding the relationship between traits there are some limitations to it. It only calculates the linear relationship between traits thus a Pearson correlation equal to zero does not mean there is no relationship between traits, and there is a possibility of non-linear relationship between traits. In addition, while calculating, it ignores the relationship between individuals and just considers the values presented for each trait. Lastly, correlations found between traits cannot be used to deduct a causation between them and just shows the magnitude and direction of traits relationships (Destefano et al., 2009; Hassler & Thadewald, 2003; Aggarwal & Ranganathan, 2016).

Genetic correlations are important estimates in breeding studies as they can show the level of pleiotropy between traits and should be considered in selection programs. Different studies looked into calculating genetic correlations between meat quality attributes with other traits to have a better understanding of traits relationship together. In genetic correlation estimation strength (>0.4 weak, 0.4-0.6 moderate and >0.6 strong), and direction as well as being favorable or unfavorable is important (Garrick & Ruvinsky, 2014). This means when a genetic correlation >0.6 is found, the association between traits are strong and changes in one trait will affect the changes on the other one. The strong genetic correlation means that direct selection for one trait will have a strong impact on the other. Moreover, it is expected that the two traits are affected by common genes. The direction of the correlation, meaning the value being negative or positive will show how these traits behave regarding each other. Positive correlation means with changes in one trait, other trait will be changing at the same direction and negative correlation shows that changes in one trait will affect the other trait in opposite direction. For example, if a trait A has strong negative genetic correlation to trait B, this means with each unit increase in trait A, trait B will decrease. Thus, animal breeders can select one of the two traits when defining genetic improvement programs focused on meat quality. This information is useful in genetic selection so researchers would have an idea of the relationship between traits, they synergy or antagonism and to find the optimum point for improving their trait of interest without sacrificing other useful traits that are already present (Cheverud, 1988).

Mateescu et al. (2015) on a study on Angus cattle reported that there are strong negative genetic correlations between WBSF with panel tenderness and connective tissue. In addition to strong correlations estimated between intramuscular fat content and panel juiciness, as well as WBSF, panel assessed tenderness and connective tissue.

Researchers working on genetic correlation on temperate breeds (including Angus, Hereford, Shorthorn, and Murray Grey) also found that there is a moderate correlation of 0.40 and 0.61 for intramuscular fat and consumer scoring tenderness, and –0.52 and –0.38 for intramuscular fat and objective measurements of tenderness WBSF. But the authors also reported that these correlations are different between different breeds. For example, in Brahman cattle we can see that there is moderate and positive genetic correlation of 0.45, 0.39 and 0.41 between the level of IMF and WBSF measurements at days 7, 14 and 21 of post-mortem aging (Garrick & Ruvinsky, 2014).

In a study on crossbred beef cattle, researchers reported strong negative genetic correlations between WBSF and tenderness, in addition to moderate correlations between tenderness and juiciness as well as weak correlations between flavor intensity and tenderness (Wheeler et al., 2001). Studies on Brahman calves (Riley et al., 2003) also reported strong negative genetic correlations between WBSF and tenderness. Furthermore, strong genetic correlations between WBSF with juiciness, connective tissue, and flavor intensity. They also stated that juiciness had strong correlation to tenderness. Hocquette et al. (2005) reviewed genetic effects on beef quality traits and reported that genetic correlation between three indices of sensory panel scoring, tenderness, juiciness and flavor is strong (0.84-0.91). Other studies (Calkins & Hodgen, 2007; Chevance et al., 2000; O'Quinn et al., 2012) showed the strong genetic correlations between fat content and flavor desirability, flavor intensity and off-flavor. This might be because of the presence of fat-soluble compounds which give meat its flavor. The reason behind positive genetic correlation to tenderness is the descriptive grading system for measuring levels of connective tissue. In order to evaluate levels of connective tissue by sensory panel, the rating on a nine point scale is as follows: 1= abundant amounts of connective tissue and 9= as the minimum amounts of connective tissue in samples (Caine et al., 2003).

Studies on calculating genetic correlations for color attributes indicated that strong correlations for lightness, moderate for Chroma and weak for Chroma existed before and after storage of the meat. They also reported significant strong correlations of tenderness with Chroma and a* in their samples (Cecchi et al., 2004a). Gagaoua et al. (2020) reviewed protein biomarkers present in beef color and tenderness and indicated that they have common molecular pathways, thus they are genetically associated together.

In general, considering genetic correlations reviewed in this section, it has been reported that WBSF has strong negative genetic correlations to tenderness, connective tissue and overall palatability. On the other hand, fat content is more related to flavor indices and lastly color attributes can be associated to sensory attributes as it has been showed that they have common biological pathways.

Regarding prediction model development in order to replace sensory panel measurements with objectively measured traits different studies used different approaches and variables in their models. But the common purpose of all of these studies was to facilitate the description of important traits for the meat industry (Price, 1995). There are many contributing factors determinant for beef sensory attributes including intrinsic and extrinsic elements. As it has been discussed before, intrinsic factors refers to properties of the meat itself and the interactions between those elements while extrinsic factors are those caused by environmental circumstances, breed, sex (Hocquette et al., 2014). In order to develop an accurate prediction model for predicting sensory attributes both should be included to produce an evaluation with enough criteria that captures most of the variations of sensory attributes (Bouyssou et al., 2000). Previous studies showed that sensory tenderness with WBSF as well as flavor indices with fat content are related (Chriki et al., 2013; Maltin, Balcerzak, Tilley, & Delday, 2003). But still just WBSF per se cannot explain all the properties consumers perceive and more studies needs to be done for more accurate prediction of sensory attributes.

To conclude, although most meat quality is determined during the early post-mortem period (i.e., colour, pH decline), genetics still plays an important role in its determination and beef quality attributes can be improved with genetic selection through generations. Objective and subjective measured traits are very important for understanding beef quality attributes. Previous research showed that there are undeniable relationship between these two sets of traits. However, further studies need to be done to have a better understanding of these relationships, their ability to be passed down in generations, their consistency through post-mortem aging and the possibility of replacing sensory panel assessment with objective measured traits. To promote genetic improvement of such traits there is a need for a huge number of phenotyped and genotyped animals, therefore more accuracy of additive genetic effect would be attainable, and accuracy has direct genetic positive relationship with genetic improvement. In addition, this information in combination with other influencing factors from different origins (farm, slaughterhouse, muscle and meat level) can be used for prediction of sensory attributes using objectively measured traits at different post-mortem aging periods.

1.3 Overall objectives and hypothesis

In this study I hypothesized that:

1. Sensory panel assessed attributes, as well as objective measured traits including WBSF, pH, fat content, and color indices (lightness, Hue and Chroma) at day 3 and 29 post-mortem are heritable and can be used for genetic selection
2. Quality attributes (objective and subjective) are consistent through post-mortem aging period and early measurements at day 3 post-mortem can be good indicators for day 29 post-mortem.
3. Sensory attributes measured in this study are phenotypically and genetically associated with objective measured traits
4. Color retail attributes (lightness, Hue and Chroma) at day 0, 2 and 4 of display life are heritable, and there are significant changes during display days in color attributes
5. Sensory attributes at day 3 and 29 post-mortem can be predicted from objectively measured traits and with including fixed effects in our model we can capture a great R-square for our prediction model.

Objectives of this study are:

1. Estimating variance components and heritability for sensory attributes and objective measured traits

2. Calculating Pearson phenotypic correlation coefficients as well as genetic correlations between sensory and objective measured traits

4. Trend analysis for color attributes in different days of retail display

5. Prediction model analysis at different post-mortem aging days and obtaining the significant elements in our models

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Chapter 2. Genetic association of meat quality attributes with sensory taste panel traits assessed at days 3 and 29 post-mortem

2.1. Introduction:

In general, the concept of meat quality is comprised of a set of properties that consumers appreciate when buying a product for different purposes, whether to use it in a household or selecting it as a precursor for producing a processed meat product. These properties include, but are not limited to, tenderness, juiciness, texture and flavor (Calkins & Hodgen, 2007). In the 2014-2018 national beef quality audit of Canadian retail beef satisfaction benchmark, it was reported that tenderness, juiciness and flavor are three determinant factors for consumer satisfaction. Moreover, it was also highlighted the fact that the number one consumer concern regarding beef quality remains meat texture, which is considered a combination of tenderness and juiciness (Beef Cattle Research Council, 2018). Reports from beef demand and consumption in Canada over the last 18 years also showed that beef consumption per capita has decreased whilst consumers are still willing to pay a premium for high-quality products (Sobool, 2015). This shows that the beef industry still needs to focus on improving meat quality and consistency leading to serve both producers in terms of increasing profitability and revenue from each animal and consumers in terms of receiving a better-quality product.

It is well known that beef quality is directly influenced by many factors prior to, during and after slaughter. Meat characteristics are associated with the muscle biology, which in fact, is controlled by the genetics, nutritional factors, and other biological elements. Among these three, additive genetic effects which can be passed down through generations, are very important requiring further studies. Thus, with genetic improvement of meat quality traits, eventually we would have populations that have good quality products and are consistent to meet the demand in the market for a good quality beef (Garrick & Ruvinsky, 2014).

Beef quality traits are complex been influenced by many genes with additive effect. Thus, it is not appropriate to evaluate meat quality related traits by using one type of measurement only. In order to have a fair assessment of beef attributes, scientists developed different methods, such as subjective sensory scoring by a trained panel or consumer assessments, as well as objective methods for example Warner-Bratzler Shear Force (WBSF), pH and fat content (Bruce & Aalhus, 2017b). For genetic evaluations, a large sample size of recorded animals is needed to accurately estimate and understand these traits leading to reliable genetic information or estimations about cattle populations.

Sensory scoring is a valid method which has been proved to be consistent (Gill et al., 2010b). However, this subjective method is time consuming, labor intensive and hard to obtain a large amount of data in a short period of time. To use this method, researchers need to train members of the panel, and prepare all samples according to the American Meat Science Association standard protocols and guidelines (Belk et al., 2015). On the other hand, there are some objective methods related to meat quality that are relatively easier in terms of performing and generating large amount of information in a shorter period of time. These methods include WBSF, meat color, and intramuscular fat content measurements. So, it is imperative to better understand the associations among subjectively and objectively measured traits leading us to describe whether the objective traits that are reliable indicators of sensory attribute traits. In addition, these findings can be used to develop prediction models, including as many variables as possible, to predict the changes of sensory traits by only assessing objectively measured traits. With that said, for the current study our hypotheses and objectives are:

2.1.1. Hypotheses:

1. Sensory traits, WBSF, fat content and pH are heritable and could be used for genetic selection.
2. Sensory traits (as our subjective measurements) are associated with WBSF, fat content and pH (as our objective measurements).
3. Evaluation of sensory traits by trained panellists at day 3 post-mortem is associated with those determined at day 29 post-mortem and can be used as early predictors for overall eating quality.
4. Fat content, WBSF and pH measured at days 3 and 29 post-mortem are phenotypically and genetically associated, and the evaluations performed at day 3 could be used as early indicators for day 29 post-mortem.
5. WBSF, fat content and pH at day 3 and day 29 post-mortem are phenotypically and genetically correlated with sensory panel evaluations on day 3 and 29 post-mortem, respectively.

2.1.2. Objectives:

The objective of the present study is to estimate variance components and heritability for sensory traits, WBSF, fat content and pH measured at day 3 and 29 post-mortem. In addition, we aim to estimate Pearson phenotypic and genetic correlations of WBSF, fat content, and pH with sensory traits measured at day 3 and day 29 post-mortem.

2.2. Material and Methods:

2.2.1. Data collection

Data for this study came from 1,200 multibreed beef cattle which were all cared for according to Canadian Council on Animal Care (2009) guidelines. These animals were sent to the federally inspected research abattoir at the Lacombe Research and Development Centre, Agriculture and Agri-Food Canada, where they were slaughtered according to protocols of commercial practices. After slaughter, the left longissimus muscle was removed, vacuum packed and chilled at 2˚C and for purpose of this study, aged for 3 and 29 days in a cooler at 2˚C (wind speed of 0.5 m s-1). For objective and subjective measurement purposes, 4 steaks (each with 25mm thickness) after 3 days and 4 steaks after 29 days of aging were used from each animal. Meat pH was measured at both time points post-mortem using Hanna HI9025C pH meter (Hannah Instruments, Mississauga, ON). For fat content measurements crude intra-muscular fat was extracted using petroleum ether (AOAC, 1995). For both fat content and pH measurements replicates of 3 samples were used.

For shear force measurements (WBSF), the steaks were cooked on an open-hearth grill (Garland Grill ED30B, Condon Barr Food Equipment Ltd., Edmonton, AB) to an internal temperature of 71 ºC. Cooked steaks were transferred to polyethylene bags then immediately put into an ice/water bath to prevent further cooking. Then they were transferred to a 4 ºC cooler and used after 24 hours for shear force measurements. For this aim, six cores each with 1.9 cm diameter per cooked steaks were cut parallel to the fiber grain using a TA-XTPlus Texture Analyzer equipped with a Warner-Bratzler shear head, then sheared with a cross head speed of 200 mm/min and a 30 kg load cell using texture Exponent 32 software (Texture Technologies Corp., Hamilton, MA).

A second cut of the steaks were used for sensory panel scoring. These steaks were also cooked as mentioned above to an internal temperature of 71 ºC then they were cut into 1.3 cm cubes (omitting connective tissue and large areas of fat). These stakes were evaluated by a trained sensory panel consisting of 8 members. Thus, eight samples per steak were prepared and presented to panel members placing into a glass jar in a circulating water bath (Lindberg/Blue Model WB1120A-1, Kendro laboratory products, Asheville, NC) and allowed to equilibrate to 71 ºC prior to evaluation. Sensory traits were ranked on a nine-point descriptive scale (American Meat Science Association, 1995). Briefly, for flavor intensity the scores ranged from 1 (extremely bland beef flavor) to 9 (extremely intense beef flavor), off-flavor intensity (1 = extremely intense off-flavor and 9 = no off-flavor) and amount of connective tissue (1 = abundant amounts of connective tissue and 9 = no connective tissue detected). Attributes collected on a nine-point descriptive scale just prior to expelling the sample included overall tenderness (1 = extremely tough and 9 = extremely tender), sustained juiciness (1 = extremely dry and 9 = extremely juicy) and overall palatability (1 = extremely undesirable and 9 = extremely desirable). These evaluations took place in a booth with good ventilation and under red lighting (124lux). Between samples distilled water and soda crackers were provided to clean the palate of any residual flavor.

2.2.2. Statistical analysis

After receiving the raw phenotypic data base, data manipulation and quality control was performed using Microsoft Excel, and R software (R Core Team, 2013). Afterwards for outlier detection a Boxplot method was used in R software and cleaned data were saved into new spread sheets.

The phenotypic correlations were estimated as Pearson's coefficients of correlations between each pair of traits by using R software. In the present study we used Evans (1996) classifications for better interpretation of the correlation results. The author recommended to consider ranges of 0.0 to 0.19 as very weak, 0.20 to 0.39 as weak, 0.4 to 0.59 as moderate, 0.60 to 0.79 as strong and 0.8 to 1.0 as very strong correlations.

The animals were genotyped using the Illumina Bovine SNP50 v3 BeadChip (50K, Illumina Inc., San Diego, CA). After receiving the raw genotype data, quality control for sample call rate (>10%), SNP call rate (10%), minor allele frequency (>1%) and departure from Hardy-Weinberg equilibrium was applied. After quality control, 37,298 SNPs and 1,156 animals remained for further analysis. All animals with both genotype and phenotypic information were selected for building a G-matrix in R software with the *Synbreed* package (Wimmer et al. 2012).

For variance components, heritability, and genetic correlation estimations the ASReml software was used (Gilmour & Gogel, 2009). An animal model was implemented including contemporary groups (comprised by animal location and birth year, feedlot group, and slaughter date) and animal sex as fixed effects. In addition, breed composition and slaughter age were included as covariates. Breed composition was estimated based on SNP genotypes by using the Admixture software. In total, 11 breed fractions were generated and then they combined into Continental or British groups to be considered as covariate in the animal model. Each group of breeds (Continental or British) have a number of traits in common. British breeds consist of Red and Black Angus, Galloway, Hereford, and Jersey, and the Continental breeds consist of Charolais, Chianina, Gelbvieh, Limousin, Maine Anjou, Simmental, Brown Swiss, and Holstein. All contemporary groups with less than 10 animals were excluded.

The single-trait animal model used to estimate variance components and the heritability of each trait can be represented as follows:

$$\boldsymbol{y} = \boldsymbol{1\mu} + \boldsymbol{Xb} + \boldsymbol{Zg} + \boldsymbol{e}$$

where $\boldsymbol{y}$ is the vector of observations; $\boldsymbol{b}$ is the vector of fixed effects; $\boldsymbol{g}$ is the vector of additive genetic effects; $\boldsymbol{e}$ is the vector of residual effects; and $\boldsymbol{X}$ and $\boldsymbol{Z}$ are incidence matrices relating $\boldsymbol{b}$, and $\boldsymbol{g}$ to $\boldsymbol{y}$. To estimate genetic correlations between traits, a bivariate animal model was used considering the same above-mentioned elements (fixed and random effects). The model can be represented as follows:

$$\begin{bmatrix} \boldsymbol{Trait1} \\ \boldsymbol{Trait2} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X1} & \boldsymbol{0} \\ \boldsymbol{0} & X2 \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta 1} \\ \beta 2 \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z1} & \boldsymbol{0} \\ \boldsymbol{0} & Z2 \end{bmatrix} \begin{bmatrix} \boldsymbol{g1} \\ g2 \end{bmatrix} + \begin{bmatrix} \boldsymbol{e1} \\ \boldsymbol{e2} \end{bmatrix}$$

where $\boldsymbol{X1}$ is the design incidence matrix for first trait's fixed effects; $\boldsymbol{X2}$ is the design incidence matrix for second trait's fixed effects; $\boldsymbol{\beta 1}$ is a vector of regression coefficients of first trait's fixed effects; $\boldsymbol{\beta 2}$ is a vector of regression coefficients of second trait's fixed effects; $\boldsymbol{Z1}$ is design incidence matrix for first trait's random effects; $\boldsymbol{Z2}$ is the design incidence matrix for second trait's random effects; $\boldsymbol{g1}$ and $\boldsymbol{g2}$ are vectors of random effects; and $\boldsymbol{e1}$ and $\boldsymbol{e2}$ are vectors of residual of observed data.

2.3. Results:

2.3.1. Descriptive statistics:

In the present study three objective measured traits of meat quality and six subjective sensory traits were evaluated at days 3 and 29 post-mortem. The descriptive statistics of these traits are outlined in Table 2.1.

2.3.2. Pearson coefficient correlations:

The Pearson's coefficient of correlations for each trait between day 3 and 29 post-mortem are presented in Table 2.2. Our results showed that fat content measured at days 3 and 29 is highly correlated (0.83) and, overall tenderness and Warner-Bratzler shear force on day 3 are moderately correlated with their measurements on day 29 post-mortem (0.5 and 0.4 respectively). However, phenotypic correlations were weak for the other traits between day 3 and 29.

Pearson's coefficient of correlations between all sensory traits with Warner-Bratzler shear force, meat pH and fat content measured at days 3 and 29 post-mortem are provided in Table 2.3. Our results suggested that overall tenderness and WBSF on day 3 post-mortem have moderate phenotypic correlations. In addition, WBSF at day 3 post-mortem is moderately correlated to overall palatability (day 3), connective tissue (day 3) and overall tenderness (day 29). Likewise, WBSF at day 29 post-mortem is moderately correlated to overall tenderness (day 3), overall palatability (day 3) and overall tenderness (day 29).

Results for Pearson correlations among sensory traits at days 3 and 29 post-mortem are shown in Table 2.4. As indicated, overall palatability and connective tissue at day 3 post-mortem are moderately correlated to overall tenderness at day 29 post-mortem.

2.3.3. Genetic parameter estimations

The additive genetic variance, residual variance and heritability estimates followed by their standard errors for sensory and objective traits (Warner-Bratzler shear force, fat content and meat pH) are presented in Table 2.5. The estimates indicated that between sensory traits, overall tenderness (day 3), overall palatability (day 3), and overall tenderness (day 29) have moderate to high heritability. In addition, WBSF (day 3), and fat content measured at both days 3 and 29 post-mortem also showed moderate to high heritability. All other sensory traits, measured at days 3 and 29 showed low heritability estimates with values ranging from 0.06 to 0.17.

2.3.4. Genetic correlations:

The genetic correlation estimates between each trait measured at days 3 and 29 are presented in Table 2.6. These results indicated that overall tenderness, overall palatability, flavour intensity, off-flavour, Warner-Bratzler shear force and fat content have strong genetic correlations between days 3 and 29 post-mortem. Thus, we can assume that there is a common genetic background that controls these traits on days 3 and 29 post-mortem and the early measurement can be used to infer about meat quality attributes at day 29 post-mortem.

Genetic correlation estimates and their standard errors between sensory taste panel traits with WBSF, meat pH, and fat content measured at days 3 and 29 post-mortem are presented in Table 2.7. The results showed that there is some strong genetic correlation of WBSF with overall tenderness measured at days 3 and 29 post-mortem (-0.88, -0.85, -0.66 and -0.87, respectively), of WBSF day 3 and 29 with overall palatability at day 3 (-0.71, and -0.69), of WBSF day 3 with connective tissue day 3 (-0.81), and of WBSF day 29 with connective tissue measured both at day 3 (-0.73) and 29 (-0.77). In addition, WBSF day 29 was highly correlated with flavor intensity at day 3 (-0.59) and 29 (-0.70). Strong genetic correlations of fat content measured at days 3 and 29 was found with flavor intensity (0.88, 0.87, 0.79 and 0.83) and off-flavor (0.74, 0.89, 0.67 and 0.75) also at both measurement days. Lastly, strong genetic correlations between fat content measured at day 3 and 29 with overall palatability day 29 (0.94, and 0.85) were estimated.

Genetic correlation estimates and their standard errors between day 3 and 29 of each sensory taste panel trait are presented in Table 2.8. Our results showed that overall tenderness (day 3) and off-flavour (day 29, 0.67), overall palatability (day 3, 0.52) as well as overall palatability (day 3) with flavour intensity (0.64) and sustained juiciness (day 29, 0.67) were highly correlated. In addition, genetic correlations between connective tissue (day 3) and overall tenderness (day 29, 0.85), flavour intensity (day 3) and overall tenderness as well as overall palatability (day 29, 0.70 and 0.80) were also of high magnitude.

2.4. Discussion:

2.4.1. Phenotype Pearson correlations

Estimation of correlations is essential for breeding purposes to draw a clear picture of how economic traits have been related to each other in a population through generations. The Pearson phenotypic correlation shows how phenotypic traits changes. If estimated values are moderate to high it means that the trait is consistent and, in our case, with different measurements at day 3 and 29 post-mortem, we can consider early measurements as good indicators for late (day 29) meat quality traits.

Phenotypic records of palatability traits, such as overall tenderness and juiciness, flavor intensity and off-flavor indices describe sample attributes from a sensory panel's perspective. Gill et al. (2010) reported that sensory scoring by a trained panel is moderately to highly consistent and this procedure was regarded as the best way for describing and assessing these complex eating quality traits. Thus, as the result of this method has been reproducible among independent studies, using these indicators of beef quality traits is considered reasonable and reliable. The data that is generated from sensory panel method has been used for estimation of phenotypic and genetic correlations of sensory traits (Leal-Gutiérrez & Mateescu, 2019). This expands our knowledge of the traits per se and their relationships together.

Caine et al. (2003) in a study on Canada's first yield grade beef carcasses after 14 days of aging, reported strong and negative Pearson correlations between overall tenderness and WBSF, in addition to moderate and negative correlation between WBSF and connective tissue and overall palatability. These results are similar to ours on both days 3 (correlation of WBSF day 3 with OT, OP and CT day 3) and 29 (correlation of WBSF day 29 with OT day 29) post-mortem, however, at day 29 post-mortem our phenotypic correlations of WBSF with CT and OP were weak.

In another study by Jeremiah et al. (2003) on Canadian AA carcasses, after 3 days of aging, strong positive phenotypic correlations between fat content and juiciness was reported. The authors also found weak correlations between fat content and overall tenderness, connective tissue, flavor intensity and overall palatability. Their results are in line with our findings on both day 3 and 29 post-mortem where we estimated weak phenotypic correlations between fat content and sensory panel attributes. The only distinction was found for juiciness, which according to them had a strong correlation to fat content but Pearson's correlation between these two traits was weak in the present study.

Shackelford et al. (1995) in a study with meat samples from crossbred beef cattle after 14 days of aging reported strong correlations between overall tenderness and connective tissue (0.76) as well as overall tenderness and juiciness (0.51). Our results are not in line with Shackelford et al. (1995), since we estimated low to moderate correlation values between overall tenderness and connective tissue and very weak correlations between juiciness and other palatability traits. These authors stated that there were weak correlations between flavor intensity and off-flavor with overall tenderness, which confirms our results.

In a study on meat quality traits in different cattle breeds (including Angus, Charolais, Limousin and Simmental), after 14 days of aging and grouping the samples into similar intramuscular fat content, correlations between WBSF and panel tenderness were reported as negative and of moderate to high magnitude (Chambaz et al., 2003). This study also stated meat pH had negative and weak correlation with panel tenderness. Both results are confirmed in the present study. Riley et al. (2003) investigated the correlations between WBSF at different days (7, 14 and 21 post-mortem) with sensory panel scoring at day 14 post-mortem in Brahman cattle. Based on their findings WBSF at day 7 had moderate to strong phenotypic correlations to itself and at day 14 and 21. Considering our results, we also found a moderate correlation between WBSF at day 3 and 29 post-mortem. In addition, Riley et al. (2003) also reported strong correlations between panel tenderness and connective tissue, as well as moderate negative correlations between WBSF (day 7, 14 and 21) with panel tenderness (day14). These results were in line with our findings, while they also reported moderate correlations between juiciness and tenderness, and of juiciness with flavor intensity, which were different from our results that indicated a weak correlation between these traits. The possible reason behind these differences can be the fact that they used a small sample size and a single breed in their study. These researchers also stated that other phenotypic correlations between sensory data were weak which agrees with our findings. Wheeler et al. (2001) in a study of crossbred beef cattle, after 7 and 14 days of aging, reported a strong and negative correlation between tenderness (day 14 post-mortem) and WBSF (day 7 and 14 post-mortem). These results were consistent comparing our findings in this study. They also reported a strong correlation between WBSF day 7 and WBSF day 14, however, our calculated correlation between WBSF day 3 and 29 were moderate. These researchers stated that they found a strong correlation between tenderness and juiciness as well, which is different from our weak correlation between juiciness and other palatability traits. Other than these mentioned correlations, Wheeler et al. (2001) also reported weak correlations between tenderness, flavor intensity, juiciness and WBSF day 3 and WBSF day 14, which confirms our findings for most of the phenotypic correlations that we calculated in this study.

In general, our study suggested that phenotypically, there was moderate to strong correlations between WBSF and overall tenderness, overall palatability, and connective tissue at days 3 and 29 post-mortem. Our results maybe differ from some other studies because of differences between and within breeds as well as different aging periods of the meat.

2.4.2. Heritability estimates

One of the questions that biologists are trying to answer regarding different traits is what proportion of the variation in a trait originates from environmental factors and how much comes from genes and their biological pathways and backgrounds. The very concept of heritability means how much a trait of interest is controlled by genes and can be passed down through generations. Heritability (in a narrow sense) can be calculated as a ratio of additive genetic variance with total phenotypic variance (sum of genetic variance and residual variance). Heritability is a dimensionless population estimate which is a useful tool for comparisons of a traits across different populations and can be used for different breeding purposes (Visscher et al, 2008). In addition, heritability estimates can be used to calculate response to selection and genetic improvement in a population for different traits.

Meat palatability traits are complex and hard to improve. These traits are controlled by many genes and a number of factors affecting them. It has been reported that most of these traits have low to moderate heritability estimates which makes it harder to improve as they are less under additive genetic effect and highly influenced by environmental effects. In addition, these traits can vary and be subjected to change with different ante and post-mortem factors (Garrick & Ruvinsky, 2014). As it has been reported in the 2018 national beef quality audit (Beef Cattle

Research Council, 2018), overall customer satisfaction of beef quality is still driven by palatability factors such as tenderness, juiciness and flavour. Furthermore, in a report by Farm Credit Canada (Sobool, 2015), it has been shown that in the past 15 years beef consumption has been reduced (per capita) while demand for buying a good quality product is still high and increasing overtime. This gap between demand and consumption originates from meat inconsistency and price. Products that are present in the market cannot meet all consumers' expectations. By promoting genetic improvement in meat quality and consistency, we can close this gap and both consumers and producers will benefit. In this study, we calculated heritability for sensory taste panel traits which are subjective traits, as well as other objectively measured meat quality attributes (WBSF, fat content, and meat pH). Providing this information is valuable to the industry and farmers so they can have the knowledge of extent of heritability of traits per se. With having economics data and correlations between traits in hand, they can develop selection index equations, predict the merit of each individual, and perform better selection programs for their herds to close the above-mentioned gap between consumption and demand. The estimations including additive genetic variance, residual variance and heritability of sensory traits and objective measured traits are presented in Table 2.5. Our results suggested that Warner-Bratzler shear force, fat content, overall tenderness and overall palatability had the highest heritability estimates among our traits, ranging from 0.27 to 0.54, and juiciness and flavor intensity had lowest heritability estimates at days 3 (0.06 and 0.15) and 29 (0.07 and 0.11) post-mortem. Our results showed that heritability estimates declined for each trait between day 3 and 29 of post-mortem aging. This is due to environmental factors effects in place which causes the reduced heritability at day 29 compared to day 3 post-mortem. These effects can namely be the external conditions during storage (temperature, humidity, velocity) or internal changes due to biochemical reactions that happens in meat during post-mortem aging.

Pratt et al. (2013) in a study of 10 different breeds and aging the meat samples for 3, 7, 14 and 21 consecutive days post-mortem also reported heritability estimates for palatability traits. Their estimate for WBSF was 0.23 and 0.42 at day 3 and 21 post-mortem which was in accordance and higher than our estimates (day 3 = 0.27 and 29 = 0.17), respectively. They also reported heritability estimates of 0.31 and 0.16 for sustained tenderness at days 3 and 21 post-mortem which were in the range and lower than our estimates comparing to overall tenderness in our results at days 3 (0.30) and 29 (0.21) post-mortem. The heritability estimates reported by these authors for sustain juiciness (0.05 at day 3 and 0.00 at day 21) and flavor intensity (0.22 at day 3 and 0.10 at day21) were in the range of our estimates. The reported range of heritability estimate for flavor intensity was higher than our results (0.15) at day 3 post-mortem.

Mateescu et al. (2015) in study on Angus sired beef after 14 days of aging reported a relatively moderate to high heritability for fat content (0.38), connective tissue (0.25), and low heritability for WBSF (0.19) and panel tenderness (0.18) and very weak heritability for juiciness (0.06). Comparing to our findings, WBSF (day 3 = 0.27 and day 29 = 0.17) and sustain juiciness (day 3 = 0.06 and day 29 = 0.07) were in the same range. Fat content (day 3 = 0.54 and day 29 = 0.44) and overall tenderness (day 3 = 0.30 and day 29 = 0.21) were lower than our estimates, and connective tissue (day 3 = 0.13 and day 29 = 0.11) was higher than our estimates.

Dikeman et al. (2005) in a study with 14 different beef breeds and aging meat samples 14 days post-mortem reported a heritability of 0.40 for WBSF, 0.37 for overall tenderness, 0.46 for juiciness and 0.07 for flavor intensity. Comparing to our results these heritability estimates were in range except for juiciness which our results showed a very low heritability (0.06 and 0.07 at day 3 and 29 post-mortem, respectively).

Riley et al. (2003) in a study on Brahman cattle aging meat samples for 7, 14 and 21 days reported lower heritability estimates for WBSF (day 7 = 0.14, day 14 = 0.14 and day 21 = 0.06) than our estimates, comparing to day 3 (0.27) and day 29 (0.17). Although their estimates on day 14 was in the range of our results for day 29 post-mortem. These authors also reported heritability estimates at day 14 post-mortem for tenderness (0.11), connective tissue (0.12), juiciness (0.05), flavor intensity (0.04), and off-flavor (0.01) traits. These estimates were lower than our findings for tenderness, flavor intensity and off-flavor at both days 3 and 29 post-mortem, but interestingly their results confirm our estimates of heritability for connective tissue and juiciness measured at both days. The reason of these differences between their results and our finding might be the fact that they used a composite *Bos taurus indicus* breed to calculate their parameters within that population.

Wheeler et al. (2001) after 7 and 14 days of aging of crossbred beef meat, estimated heritability for WBSF at day 7 (0.29) and day 14 (0.24), which our estimates were in the range of these researchers' findings. They also reported heritability estimates for palatability traits at day 14 post-mortem as following: tenderness (0.22), juiciness (0.09), and flavor intensity (0.07), which is in line with our estimates for the same traits.

Hocquette et al. (2005) in a review on different studies in USA universities (Texas, Colorado, Florida and Louisiana) on meat quality attributes, stated that the heritability estimates for tenderness is, on average, equal to 0.24. The studies included in their review also showed low heritability estimates for juiciness (0.11) and flavor (0.09). In addition, the authors also reported that heritability for intramuscular fat content was, on average, equal to 0.49 in nine other studies. The reported results also confirm the heritability ranges that we obtained in our study.

Lambe and Simm (2014) reported low heritability for juiciness, flavor and ultimate pH ranging from 0 to 0.25, for tenderness ranging from low to moderate (<0.5), and for shear force and fat content ranging from moderate to high (>0.25) magnitudes. Our heritability estimates were within the ranges obtained by Hocquette et al. (2005).

The reason for differences in heritability estimations, comparing different studies, are most likely the population structure, as different breeds have different connective tissue and muscle fiber attributes, which per se will affect features like meat tenderness and flavor. Heritability is feature of population and it is a function of factors that are specific for each population. Some of these factors are allele frequencies, the amount of allele effect on the trait and environmental-related factors. The heritability of a trait in a population does not necessarily predict heritability in another population but they tend to be similar (Wray & Visscher, 2008). In addition, differences between studies as well as different periods of aging of the meat (some 14 days, some 21 and in our study 29 days post-mortem) are important factors affecting the studied traits.

2.4.3. Genetic correlations

A single gene may affect more than one economic trait. There may be many genes that affect two or more traits. This phenomenon is called pleiotropic effect of genes. Genetic correlation of two traits is a measure that shows the direction and weight of two trait changes due to genetic causes, which can show pleiotropic relationships between genes, casual overlap or a common biochemical pathway or the possibility of linkage disequilibrium. The genetic correlation has application in animal breeding when fitting the selection index (Hazel, 1943). Moreover, it increases our knowledge of how the genetic background influences economic traits and our understanding of biological origin of complex traits.

In this study, we aimed to understand the genetic correlations between objective and subjective traits. By calculating genetic correlations between objective measured traits and subjective measured traits we aimed to understand the relationships between traits to know how much selection for one trait would affect all other traits and in which direction (positive or negative). This valuable information is essential for accurate selection of animals as well as gaining pre-knowledge and results that can be used in prediction models to answer the question about possibility of replacing subjective traits by objectively measured traits This would be an important approach since subjective traits (such as sensory panel scoring for meat attributes) are more expensive, labour-intensive, and time-consuming to be recorded than objective traits. Wheeler et al. (2001) in a study on crossbred beef cattle after 7 and 14 days of aging, (both days used for WBSF measurements and only day 14 used for sensory evaluations), found that there is a strong genetic correlation between WBSF day 7 and day 14 (0.88). This is in conformance with our results where we found a strong correlation between WBSF on day 3 and 29 (0.88). These researchers also reported a strong negative correlation between tenderness and WBSF at days 7 and 14 post-mortem, which is also in accordance with our results, where we found a strong negative correlation between WBSF days 3 and 29 post-mortem with overall tenderness. In addition, Wheeler et al. (2001) stated that there is a moderate genetic correlation between tenderness and juiciness, and weak correlations between tenderness and flavor intensity, which were different than our findings.

In another study on Brahman calves after 14 days of aging for sensory and 7, 14 and, 21 days post-mortem for WBSF measurements, Riley et al. (2003) reported strong genetic correlations between WBSF days 7, 14 and 21 post-mortem. They also stated that there are strong negative correlations between panel tenderness as well as connective tissue and flavor intensity with shear force on days 3, 14 and 21 post-mortem. All these findings are in accordance with our results. These researchers also reported strong correlations between juiciness and WBSF, juiciness and tenderness, which was in contrast with our findings (Riley et al., 2003).

Mateescu et al. (2015) in a study on Angus breed cattle and after 14 days of aging post-mortem in USA reported that WBSF have a strong negative correlation to panel tenderness as well as connective tissue. The authors also reported a strong correlation between intramuscular fat content and juiciness, in addition to strong correlations between connective tissue with panel tenderness. Our results are similar to Mateescu et al. (2015).

In a study on temperate and adopted breeds in Australia after 14 days of aging, Reverter et al. (2003) reported a strong negative correlation between tenderness and shear force which was confirmed by our results. They also reported a high genetic correlation between intramuscular fat content and tenderness, which was different from our findings in this study, where we did not find a strong correlation between fat content and tenderness (both on days 3 and 29).

Johnston et al. (2003) in a study similar to Reverter et al. (2003), with a consumer assessed traits, reported a strong genetic correlation between flavor intensity and juiciness of the meat, which is similar to our results, where we found a moderate to high genetic correlation between flavor intensity on day 3 and juiciness on day 29 post-mortem.

Hocquette et al. (2005) in a review about genetic effects on beef attributes, stated that genetic correlation between tenderness, juiciness and flavor score is strong (ranging from 0.84 to 0.91), which is in conformance with our results, as we found strong genetic correlations between overall tenderness at day 3 and flavor intensity at day 29 post-mortem.

In a study by O'Quinn et al. (2012) on consumer assessment of beef with different levels of fat reported that they have related flavor desirability of the meat with increasing intramuscular fat content. At the same time, other studies (Calkins & Hodgen, 2007; Chevance et al., 2000) indicated that increased fat content is related to off-flavor properties of the meat due to presence of volatile compounds originated from fat oxidation. In the present study we reported strong genetic correlation of fat content with flavor intensity (ranging from 0.79 to 0.88) and off-flavor (ranging from 0.67 to 0.89) which is in line with other studies and confirm the association between fat content and meat flavor.

Overall, in this study we found some interesting results in terms of genetic correlation which showed that many sensory traits (subjective) are genetically related to objective measured traits. For example, fat with flavor intensity and off-flavor or WBSF with connective tissue, tenderness and overall palatability are highly correlated in our crossbred beef cattle population. These results indicate that we can potentially use the objective measured traits in prediction models to predict sensory attributes of the meat.

Furthermore, our findings showed that some of these traits are highly correlated together through time while some, such as connective tissue, interestingly showed a lower genetic correlation between day 3 and 29. This is an indication that shows genetic background and pathways are changing through time for this trait and are changing through aging period of the meat. These findings can also be potentially used in different models including more data, to predict the changes in sensory or objective measured traits. So, with only one set of measurement at day 3 post-mortem, producers would know the change patterns in the same traits after 29 days of aging post-mortem.

2.5. Conclusion:

Considering that overall tenderness, overall palatability, fat content and shear force on day 3 and connective tissue and fat content on day 29 post-mortem have moderate to high heritability, these traits will show a better response to selection being considered good target traits to perform genetic improvement of meat quality in crossbreed animals. The expected result will also address the need to improve meat tenderness which is the number one quality concern by consumers.

The phenotypic correlations that have been found in this study were mainly of low magnitude. In general, fat content, overall tenderness, overall palatability and WBSF had strong to moderate correlations with themselves between day 3 and 29 post-mortem. In addition, some moderate to strong genetic correlations between WBSF and overall tenderness, overall palatability, and connective at day 3 and 29 post-mortem were found. These results indicates that meat palatability attributes are not consistent and change over time and early measurements for mentioned traits (at day 3 post-mortem) are not good indicators of their changes after aging period (day 29 post-mortem).

Most of genetic correlations found in this study were strong and favorable, which shows that there are probably similar genes with additive effect and molecular pathways influencing these traits. Hence, based on results found in this study a set of indicators can be used for direct selection on overall tenderness, overall palatability, flavour intensity, off-flavour, Warner-Bratzler shear force and fat content can be recommended, as they have strong (positive or negative) in other corresponding traits. These results can be used both for developing prediction models for palatability attributes from subjectively and objectively measured trays as well as helpful for having a better understanding of the relation of these traits together for performing selection in breeding programs.

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Table 2. 1 Descriptive statistics of objective and subjective traits

Traits	N	Mean	SD	Min	Max	CV%
Objectively measured traits						
Warner-Bratzler shear force, day 3	1,153	7.74	1.66	3.37	12.42	21
Fat content, day 3	1,131	3.25	1.13	0.76	6.53	34
Meat pH, day 3	1,152	5.57	0.07	5.36	5.79	1
Warner-Bratzler shear force, day 29	1,136	4.78	0.78	2.64	7.01	16
Fat content, day 29	1,123	3.77	1.30	0.72	7.54	34
Meat pH, day 29	1,139	5.62	0.09	5.38	5.85	1
Subjectively measured traits						
Flavor Intensity, day 3	1,149	5.36	0.40	4.38	6.38	7
Off-flavour, day 3	1,143	7.95	0.47	6.63	9.00	6
Connective tissue, day 3	1,114	8.11	0.37	7.13	9.00	4
Overall tenderness, day 3	1,147	5.76	0.93	3.25	7.75	16
Sustain juiciness, day 3	1,153	5.46	0.41	4.25	6.57	7
Overall palatability, day 3	1,133	4.88	0.60	3.33	6.43	12
Flavor Intensity, day 29	1,159	5.47	0.42	4.43	6.63	7
Off-flavour, day 29	1,145	7.93	0.45	6.71	9.00	5
Connective tissue, day 29	1,138	8.36	0.26	7.63	9.00	3
Overall tenderness, day 29	1,133	6.72	0.55	5.14	8.25	8
Sustain juiciness, day 29	1,146	5.40	0.44	4.29	6.57	8
Overall palatability, day 29	1,153	5.11	0.53	3.63	6.50	10

Number of animals (N), phenotypic mean, standard deviation (SD), Minimum value (Min), Maximum value (Max), Coefficient of variation (CV).

Table 2. 2 Estimates of phenotypic correlations with Pearson's coefficient of correlation (*r*) between each pair of the same trait measured at day 3 and 29 post-mortem.

Traits	***r* ± SE**
Overall tenderness	$0.50 \pm 0.02^{***}$
Overall palatability	$0.33 \pm 0.02^{***}$
Connective tissue	$0.22 \pm 0.02^{***}$
Flavor Intensity	$0.25 \pm 0.02^{***}$
Off-flavour	$0.19 \pm 0.02^{***}$
Sustain juiciness	$0.23 \pm 0.02^{***}$
Warner-Bratzler shear force	$0.40 \pm 0.02^{***}$
Fat content	$0.83 \pm 0.009^{***}$
Meat pH	$0.13 \pm 0.02^{***}$

***p-value < 0.01

Table 2. 3 Estimates of phenotypic correlations with Pearson's coefficient of correlation (*r*) between sensory and WBSF, pH, fat content measured at days 3 and 29 post-mortem.

Trait[1]	OT_3	OP_3	CT_3	FI_3	OF_3	SJ_3	OT_29	OP_29	CT_29	FI_29	OF_29	SJ_29
WBSF_3	-0.62 ± 0.01	-0.43 ± 0.02	-0.45 ± 0.02	-0.20 ± 0.02	-0.14 ± 0.02	-0.10 ± 0.02	-0.40 ± 0.02	-0.19 ± 0.02	-0.18 ± 0.02	-0.16 ± 0.02	-0.09 ± 0.02	-0.15 ± 0.02
FAT_3	0.19 ± 0.02	0.20 ± 0.02	0.17 ± 0.02	0.23 ± 0.02	0.07 ± 0.03	0.14 ± 0.02	0.13 ± 0.02	0.27 ± 0.02	-0.002 ± 0.03	0.30 ± 0.02	0.14 ± 0.02	0.23 ± 0.02
PH_3	-0.11 ± 0.02	-0.05 ± 0.02	-0.07 ± 0.02	-0.01 ± 0.02	0.08 ± 0.02	0.01 ± 0.02	-0.08 ± 0.02	-0.09 ± 0.02	-0.07 ± 0.02	-0.08 ± 0.02	-0.11 ± 0.02	-0.02 ± 0.02
WBSF_29	-0.46 ± 0.02	-0.40 ± 0.02	-0.29 ± 0.02	-0.21 ± 0.02	-0.14 ± 0.02	-0.13 ± 0.02	-0.54 ± 0.02	-0.23 ± 0.02	-0.26 ± 0.02	-0.19 ± 0.02	-0.14 ± 0.02	-0.19 ± 0.02
FAT_29	0.15 ± 0.02	0.17 ± 0.02	0.15 ± 0.03	0.21 ± 0.02	0.07 ± 0.03	0.12 ± 0.02	0.12 ± 0.03	0.26 ± 0.02	-0.03 ± 0.03	0.27 ± 0.02	0.13 ± 0.02	0.22 ± 0.02
PH_29	-0.07 ± 0.02	0.03 ± 0.03	-0.20 ± 0.02	0.06 ± 0.02	0.13 ± 0.02	0.17 ± 0.02	-0.06 ± 0.02	0.05 ± 0.02	-0.12 ± 0.02	-0.05 ± 0.02	0.03 ± 0.02	0.12 ± 0.02

[1]OT= overall tenderness; OP= overall palatability; CT= connective tissue; FI= flavor Intensity; OF= off-flavour; SJ= sustain juiciness; WBSF = Warner-Bratzler shear force; FAT= fat content; pH= meat pH; Days 3 and 29 post-mortem.

Table 2. 4 Estimates of phenotypic correlations with Pearson's coefficient of correlation (r) between sensory traits at days 3 and 29 post-mortem.

Traits[1]	OT 29	OP 29	CT 29	FI 29	OF 29	SJ 29
OT 3	0.50 ± 0.02	0.23 ± 0.02	0.22 ± 0.02	0.17 ± 0.02	0.14 ± 0.02	0.17 ± 0.02
OP 3	0.39 ± 0.02	0.33 ± 0.02	0.13 ± 0.02	0.24 ± 0.02	0.21 ± 0.02	0.21 ± 0.02
CT 3	0.38 ± 0.02	0.07 ± 0.03	0.22 ± 0.02	0.07 ± 0.03	0.01 ± 0.03	0.06 ± 0.03
FI 3	0.18 ± 0.02	0.26 ± 0.02	0.03 ± 0.02	0.25 ± 0.02	0.17 ± 0.02	0.19 ± 0.02
OF 3	0.14 ± 0.02	0.23 ± 0.02	-0.02 ± 0.03	0.14 ± 0.02	0.19 ± 0.02	0.14 ± 0.02
SJ 3	0.15 ± 0.02	0.18 ± 0.02	-0.04 ± 0.02	0.13 ± 0.02	0.13 ± 0.02	0.23 ± 0.02

[1] OT= overall tenderness; OP= overall palatability; CT= connective tissue; FI= flavor Intensity; OF= off- flavour; SJ= sustain juiciness; Days 3 and 29 post-mortem.

Table 2. 5 Genetic parameter estimation for sensory and objectively measured traits at day 3 and 29 post-mortem

Trait	$\sigma_a^2 \pm$ SE	$\sigma_e^2 \pm$ SE	$h^2 \pm$ SE
Objectively measured traits			
Warner-Bratzler shear force, day 3	0.648 ± 0.174	1.723 ± 0.158	0.273 ± 0.068
Fat content, day 3	0.486 ± 0.080	0.410 ± 0.060	0.542 ± 0.074
Meat pH, day 3	0.0008 ± 0.0003	0.003 ± 0.0003	0.194 ± 0.072
Warner-Bratzler shear force, day 29	0.090 ± 0.035	0.430 ± 0.035	0.173 ± 0.066
Fat content, day 29	0.567 ± 0.110	0.694 ± 0.088	0.449 ± 0.076
Meat pH, day 29	0.0002 ± 0.0002	0.004 ± 0.0003	0.051 ± 0.055
Subjectively measured traits			
Flavor Intensity, day 3	0.022 ± 0.008	0.122 ± 0.009	0.157 ± 0.058
Off-flavour, day 3	0.033 ± 0.013	0.167 ± 0.013	0.167 ± 0.063
Connective tissue, day 3	0.016 ± 0.007	0.101 ± 0.007	0.137 ± 0.062
Overall tenderness, day 3	0.231 ± 0.056	0.525 ± 0.050	0.306 ± 0.068
Sustain juiciness, day 3	0.009 ± 0.008	0.139 ± 0.009	0.061 ± 0.054
Overall palatability, day 3	0.074 ± 0.021	0.241 ± 0.020	0.234 ± 0.065
Flavor Intensity, day 29	0.018 ± 0.009	0.137 ± 0.009	0.119 ± 0.056
Off-flavour, day 29	0.018 ± 0.011	0.167 ± 0.012	0.100 ± 0.060
Connective tissue, day 29	0.007 ± 0.004	0.059 ± 0.004	0.111 ± 0.061
Overall tenderness, day 29	0.055 ± 0.017	0.205 ± 0.016	0.212 ± 0.063
Sustain juiciness, day 29	0.013 ± 0.009	0.162 ± 0.011	0.077 ± 0.053
Overall palatability, day 29	0.030 ± 0.015	0.217 ± 0.016	0.124 ± 0.059

σ_a^2= Additive genetic variance; σ_e^2= Residual variance; h^2= heritability; SE= Standard error

Table 2. 6 Genetic correlations estimates and their standard error between day 3 and day 29 for each trait

Traits	Genetic Correlation ± SE
Overall tenderness	0.89 ± 0.10
Overall palatability	0.92 ± 0.21
Connective tissue	0.53 ± 0.29
Flavor Intensity	0.96 ± 0.35
Off-flavour	0.89 ± 0.36
Sustain juiciness	1.30 ± 0.87
Warner-Bratzler shear force	0.88 ± 0.15
Fat content	0.95 ± 0.02
Meat pH	1.50 ± 0.86

Table 2. 7 Genetic correlation estimates and their standard errors between sensory taste panel traits and WBSF, meat pH, and fat content at days 3 and 29 post-mortem

Traits[1]	OT 3	OP 3	CT 3	FI 3	OF 3	SJ 3	OT 29	OP 29	CT 29	FI 29	OF 29	SJ 29
WBSF 3	-0.88 ± 0.08	-0.71 ± 0.13	-0.81 ± 0.18	-0.47 ± 0.22	-0.39 ± 0.22	0.18 ± 0.34	-0.85± 0.11	-0.18 ± 0.24	-0.49 ± 0.23	-0.34 ± 0.25	0.04 ± 0.27	-0.52 ± 0.29
WBSF 29	-0.66 ± 0.14	-0.69 ± 0.17	-0.73 ± 0.20	-0.59 ± 0.26	-0.45 ± 0.26	-0.61 ± 0.48	-0.87 ± 0.11	-0.47 ± 0.28	-0.77 ± 0.21	-0.70 ± 0.26	-0.43 ± 0.34	-0.55 ± 0.37
FAT 3	0.14 ± 0.13	0.41 ± 0.14	0.22 ± 0.20	0.88 ± 0.13	0.74 ± 0.17	0.40 ± 0.31	0.16 ± 0.15	0.94 ± 0.16	-0.15 ± 0.21	0.87 ± 0.14	0.89 ± 0.25	0.90± 0.21
FAT 29	0.23 ± 0.14	0.42 ± 0.15	0.29 ± 0.21	0.79 ± 0.14	0.67 ± 0.17	0.65 ± 0.34	0.09 ± 0.17	0.85 ± 0.18	-0.39 ± 0.22	0.83 ± 0.16	0.75 ± 0.28	0.95 ± 0.21
pH 3	-0.16 ± 0.20	-0.07 ± 0.23	-0.14 ± 0.29	-0.11 ± 0.28	0.38 ± 0.25	-0.01 ± 0.42	-0.01 ± 0.24	0.31 ± 0.30	-0.09 ± 0.32	0.08 ± 0.30	0.44 ± 0.34	-0.15 ± 0.37
pH 29	-0.25 ± 0.40	-0.10 ± 0.40	-0.71 ± 0.60	-0.37 ± 0.59	-0.38 ± 0.47	1.16 ± 0.45	-0.12 ± 0.39	0.35 ± 0.53	-0.74 ± 0.53	-0.009 ± 0.50	0.02 ± 0.57	0.48 ± 0.62

[1] OT= overall tenderness; OP= overall palatability; CT= connective tissue; FI= flavor Intensity; OF= off- flavour; SJ= sustain juiciness; WBSF = Warner-Bratzler shear force; FAT= fat content; pH= meat pH; Days 3 and 29 post-mortem.

Table 2. 8 Genetic correlation estimates and their standard errors between each sensory taste panel trait measured at day 3 and 29 post-mortem.

Traits[1]	OT 29	OP 29	CT 29	FI 29	OF 29	SJ 29
OT 3	0.89 ± 0.10	0.52 ± 0.23	0.32 ± 0.23	0.48 ± 0.24	0.67 ± 0.29	0.26 ± 0.29
OP 3	1.00 ± 0.12	0.92 ± 0.21	0.33 ± 0.25	0.64 ± 0.26	1.26 ± 0.41	0.67 ± 0.29
CT 3	0.85 ± 0.18	0.60 ± 0.31	0.53 ± 0.29	0.33 ± 0.33	0.62 ± 0.39	0.08 ± 0.40
FI 3	0.70 ± 0.24	0.80 ± 0.31	0.16 ± 0.33	0.96 ± 0.35	1.06 ± 0.40	0.61 ± 0.32
OF 3	0.74 ± 0.24	0.79 ± 0.28	0.09 ± 0.33	0.88 ± 0.26	0.89 ± 0.36	1.12 ± 0.36
SJ 3	0.39 ± 0.41	1.35 ± 0.57	0.19 ± 0.50	0.25 ± 0.47	1.19 ± 0.41	1.30 ± 0.87

[1] OT= overall tenderness; OP= overall palatability; CT= connective tissue; FI= flavor Intensity; OF= off- flavour; SJ= sustain juiciness.

Chapter 3. Genetic associations between meat color measured at days 3 and 29 post-mortem with sensory taste panel traits in crossbred beef cattle

3.1. Introduction:

Visual and sensory aspects of the meat are two important factors that indicates whether a product is good for consumption by consumers. In particular, color of the meat plays an important role in consumers' choice. Consumers often times consider bright red color as an indicator of freshness of the product and anything visually different from that will be discriminated against, as consumers consider discolorations as signs of spoilage of the product. Records showed that in USA alone, 15% of displayed products in the retail case are discounted due to discoloration which results in $1 billion revenue loss annually in this section (Smith et al., 2000; Suman & Joseph, 2013). On the other hand, high variability has been found for sensory attributes, which results in consumer dissatisfaction. In recent years, consumer's interest shifted more toward a safe, ethical, wholesome and good quality product. Among these qualification criteria, eating quality has a significant importance, especially tenderness and flavor of the product (Grunert, Bredahl, & Brunsø, 2004; Miller, Huffman, Gilbert, Hamman, & Ramsey, 1995). As both sensory attributes and meat color are important traits, researchers and the beef industry are interested to improve both aiming to enhance the quality of the products in the market while increasing profitability at the same time.

Considering that color measurements are non-invasive, easy to apply, and a less time-consuming method compared to sensory panel scoring, maybe we can predict sensory attributes from color measurements, and thus replace the need for them. For developing prediction models in this regard, first we need to have knowledge of genetic and phenotypic associations as well as heritability of these traits. In addition, the correlation estimates will determine if it could be beneficial to use objective measured traits such as color measurements to indirectly predict meat sensory attributes. This information can be useful to reduce inconsistency in the product both color and sensory wise.

One other important aspect that the meat industry focuses on is retail shelf life of meat products. Shelf life can be defined as a period of time starting from packaging until it has been purchased by the end user. This is a period in which product is still acceptable and before it has become unacceptable for consumption. These characteristics include color, texture, sensory attributes and appearance (Singh & Singh, 2005). However, the color of a product while presenting in retail display, will change fast, although the product is still good for consumption (not necessarily spoiled), it will be regarded as not qualified or undesired product. Color establishment in meat is a complex matter, which in short originates from muscle pigments, namely myoglobin (producing bright red color of the meat when bonded with oxygen), hemoglobin and cytochrome (Suman & Joseph, 2013). The undesired color change that happens in packaged meat products during display is due to metmyoglobin (oxidized form of myoglobin and brown in color) formation in the meat. So, if we can find the optimum number of days for shelf life in which the color changes are not yet significant, we can help producers and retailers to have knowledge from which point and time the product on display will become discriminated against.

Overall, achieving a consistent meat product regarding sensory attributes with optimum potential meat color attributes post-mortem during retail display, are important. This will result in both consumer satisfaction and economic improvements. With these in mind, the hypotheses and objectives of this study are:

3.1.1. Hypotheses:

1. Sensory traits and color indices (L*, Hue and Chroma) are heritable, and they can be useful for genetic improvement.
2. Sensory traits are correlated to color indices (L*, Hue and Chroma).
3. Color indices (L*, Hue and Chroma) measurements at day 3 are phenotypically and genetically related to day 29 post-mortem and can be used as early indicators of meat quality in beef.
4. Color indices (L*, Hue and Chroma) at day 3 and day 29 post-mortem are phenotypically and genetically associated with sensory taste panel evaluations (subjective measured traits) on days 3 and 29 post-mortem, so meat colors can be good indicators for sensory panel scoring and can be used to replace subjective methods.
5. Retail traits (L*, Hue and Chroma) in different shelf life days (0, 2 and 4) are heritable and can be used for genetic improvement of meat quality.
6. There are significant changes between retail traits (L*, Hue and Chroma) along time, between different shelf life days (day 0, 2 and 4).

3.1.2. Objectives:

The objectives of this study are to estimate variance components and heritability for meat color traits (L*, Hue, Chroma) measured at day 3 and 29 post-mortem, and for retail display traits (L*, Hue, Chroma) measured at different shelf life days (0, 2 and 4). Furthermore, our goal here is to accurately estimate phenotypic and genetic correlations between color traits (L*, Hue, Chroma) and sensory traits measured at day 3 and day 29 post-mortem. In addition, we aimed to use retail traits (L*, Hue, Chroma) for the same samples, and with least square means estimates examine the trend of these traits and their changes along time between different shelf life days (0, 2 and 4).

3.2. Methods:

3.2.1. Data collection:

Sample collection was the same as described in Chapter 2. For color indices (L*, Hue and Chroma) measurements one of the four steaks described in chapter 2 was used. For this aim, steaks were placed into a polystyrene tray with a dri-loc pad, overwrapped with oxygen permeable film (8000 mL m-2 24 h-1; Vitafilm choice wrap; Goodyear Canada Inc.) then they were exposed to air for 20 min and color measurements took place with the Minolta CR-300 with Spectra QC-300 Software (Minolta Canada Inc., Mississauga, ON). Primarily the color measurements were a*, b* and L* and then they were converted to Hue and Chroma.

For retail traits (L*, Hue and Chroma) measurements took place between different shelf life days (0. 2 and 4). One of the 4 steaks was used for this purpose, storage method was the same as mentioned above, and then samples stored in a retail display case at 1ºC for assessment of retail storage life. On each day (0, 2 and 4) color measurements for L*, a* and b* were determined from three surface locations on steaks after exposing to atmospheric oxygen for 20 min using the Minolta CR-300 with Spectra QC-300 Software (Minolta Canada Inc., Mississauga, ON). Then these measurements were converted to Hue and Chroma (Hunt et al., 2012).

3.2.2. Data analysis:

Data arrangement and outlier detection method was performed on all datasets as described in chapter 2.

Data analysis for color indices (L*, Hue and Chroma) on day 3 and 29 post-mortem for this chapter was the same as described in chapter 2. Briefly, phenotype Pearson's coefficient of correlation was calculated using R software for our target traits. In addition, univariate and bivariate animal models were used to estimate variance components, heritability estimates and genetic correlations using ASReml software. The animal models used for univariate and bivariate analyses, as well as all fixed effects and random effects considered were mentioned in chapter 2.

For trend analysis of retail data (L*, Hue and Chroma) along time a mixed model was implemented in R software and the least square means for each trait along time (0, 2 and 4 days of shelf life) was obtained. The model can be represented as follow:

$$\boldsymbol{Y_{ij} = \mu + CG_i + Sex_i + BC_i + Sla\ age_i + Time_{ij} + e_{ij}}$$

Where $\boldsymbol{Y_{ij}}$ is observation of *i*th animal at *j*th time; $\boldsymbol{\mu}$ is the population mean; $\boldsymbol{CG_i}$ is the contemporary grouping of *i*th animal; $\boldsymbol{BC_i}$ is breed composition (British and Continental) of *i*th animal; $\boldsymbol{Sla\ age_i}$ is slaughter age of *i*th animal; $\boldsymbol{Time_{ij}}$ is shelf life (days 0, 2 and 4) for *i*th animal at *j*th time and $\boldsymbol{e_{ij}}$ is residual of the model for *i*th animal at *j*th time

3.3. Results:

3.3.1. Descriptive statistics:

Descriptive statistics for three quality color traits (L*, Hue and Chroma) measured at days 3 and 29 post-mortem, and for three retail traits (L*, Hue and Chroma) measured at days 0, 2 and 4 of shelf life are shown in Table 3.1 and 3.2.

3.3.2. Phenotype Pearson correlations:

The Pearson's correlation coefficients of each color trait between day 3 and 29 post-mortem are presented in Table 3.3. Our results suggested that lightness and Hue of the meat are moderately correlated except for Chroma that is not correlated to itself between days 3 and 29 post-mortem.

The correlations of color indices (L*, Chroma and Hue) with sensory taste panel traits at days 3 and 29 post-mortem are shown in Table 3.4.

The results from this study show that the phenotypic correlations were all weak. Lightness at day 3 with overall tenderness and connective tissue both at day 3 (0.19 and 0.27 respectively), lightness at day 29 with connective tissue at day 3, and overall tenderness at day 29 (0.21 and 0.19 respectively), were all weak. Similarly, the correlations of Chroma at day 3 with overall tenderness at day 3, overall palatability at day 3 and overall tenderness at day 29 were all weak (0.29, 0.22 and 0.20, respectively).

3.3.3. Genetic parameter estimations:

The genetic parameter estimations for color indices (L*, Chroma and Hue) at days 3 and 29 post-mortem are presented in Table 3.5 followed by their standard errors. Our findings suggests that lightness (0.49 at day 3, and 0.27 at day 29 post-mortem) and Hue (0.58 at day 3, and 0.34 at day 29 post-mortem) are moderate to highly heritable. On the other hand, the estimates for Chroma were low at days 3 and 29.

The results for additive genetic variance, and residual variance in addition to heritability estimations for retail traits (L*, Chroma and Hue) in different shelf life days are presented in Table 3.6. Our findings showed that all retail traits had negligible heritability indicating that they are more affected by environmental effects than additive genetic components.

3.3.4. Genetic correlations:

Genetic correlations between day 3 and 29 post-mortem for each color trait, and the correlations of color indices with sensory taste panel traits are presented in Tables 3.7 and 3.8 respectively. Our findings regarding genetic correlations of each color index between day 3 and day 29 post-mortem, suggests that lightness and Hue have strong genetic correlations.

The genetic correlation estimations between sensory data and color measurements shows that lightness of the meat (day 3) has moderate correlations to connective tissue (day 3). In addition to that, Chroma (day 3) with overall tenderness (day 3), and flavor intensity (day 3) are moderately correlated, as well as a strong correlation between Chroma (day 3) and connective tissue (day 3) were found. Furthermore, our findings indicate that Chroma index (day 29) had strong correlation to off-flavor and overall palatability (both at day 29) and is moderately correlated to overall palatability (day 3).

3.3.5. Trend analysis for retail traits (L*, Hue and Chroma) in different shelf life days (0, 2 and 4)

Results for trend analysis of retail traits including L*, Chroma and Hue indices, measured at days 0, 2 and 4 of shelf life are presented in Figures 3.1, 3.2 and 3.3 respectively. In addition, p-values for differences between days for these traits are presented in Tables 3.9, 3.10 and 3.11.

Trend analysis for lightness between different shelf life days (Figure 3.1 and Table 3.9), showed the changes in brightness of the meat along time and their significances. Our findings suggested that there were significant changes between day 0 and 4, as well as days 2 and 4 of the shelf life. In addition, a significant decrease in lightness of the meat from day 2 to day 4 has been observed.

The trend analysis for Chroma between different shelf life days showed that differences between days 0 and 4, and between days 2 and 4 of the shelf life are significant, and there is an important decrease in color quality between day 2 and 4 of shelf life (Figure 3.2 and Table 3.10).

Lastly, results from trend analysis for Hue between different shelf life days showed that there are significant changes between day 0 and 4, and day 2 and 4 of shelf life, and there is a significant decrease from day 2 to 4 of shelf life in the Hue index as well (Figure 3.3 and Table 3.11).

3.4. Discussion:

3.4.1. Pearson phenotypic correlation:

Phenotypic correlations are one of the important statistical parameters that help breeders to understand the relationship among economically important traits that has been set during generations. In the beef industry, of most important economic traits, sensory attributes as well as color of the meat can be mentioned. Sensory traits such as tenderness, flavor and texture are important in consumer's acceptability of a product (Miller et al. 1995). In addition, color of the meat has an important role in consumer's choice for purchasing a product as it is an attribute that they can easily judge (Suman & Joseph, 2013).

As mentioned previously, sensory measurements are labor intensive, time consuming and hard to obtain large amount of data in a short period of time. In order to help differentiate palatable beef from low quality products without having to go through sensory evaluations, researchers are looking for some objective measured traits (for example color measurements, which is non-invasive and takes less time) that are associated with subjective traits. If associations between these traits could be found, with developing prediction models in the future, sensory attributes of a meat product can be predicted from color measurements. In the current study, we calculated

Pearson phenotypic correlations and genetic correlations between sensory and color traits. The results for phenotype correlations between sensory taste panel traits and color (L*, Chroma and Hue) measured at day 3 and 29 post-mortem are presented in Table 3.3 and 3.4.

Our finding suggests that the correlations between lightness (day 3 and 29 post-mortem) and overall tenderness (day 3 and 29 respectively) are weak (still higher than other phenotypic correlations among our results). Similarly, weak correlations between lightness and flavor intensity and juiciness were found. We also found weak correlations (although higher values than other phenotypic correlations) between Chroma (day 3) and overall tenderness (day 3 and 29 post-mortem).

Similarly Wulf and Page (2000) in a study on 100 beef carcasses in USA after 7 days of aging reported a moderate correlation between lightness and beef tenderness, and weak correlations among lightness with flavor intensity and juiciness. These researchers also reported moderate correlations between a* and b* values with tenderness, in addition to weak correlations among them with flavor intensity and juiciness.

In different studies on temperate and tropically adapted breeds, after 14 days of aging post-mortem, researchers reported weak correlations between tenderness and lightness, in addition to weak correlations between tenderness and a* index in both above-mentioned breed types (Johnston et al., 2003; Reverter et al., 2003). These results are in conformance with our findings as our phenotypic correlations mostly found to be weak between sensory and color attributes.

In another study, Girard et al. (2012) worked with crossbred beef cattle aging meat samples for 24 hours and 7 days, measured connective tissue levels from shear force measurements on eye of round and top sirloin. The authors reported weak phenotypic correlations of lightness, Chroma and Hue with connective tissue in eye of round and moderate correlations between them in top sirloin. Although measurements in their study did not take place with sensory panel, they still give us an idea about Pearson's phenotypic relationship between connective tissue and color indices. In the present study, our results suggested that sensory determined connective tissue and Lightness, Chroma and Hue also had weak correlations.

In another study on South African cattle using Angus, Charolais, Brahman and other breeds, Modika et al. (2015) reported weak correlations between L*, Chroma and Hue with texture and fiber separation of the meat (evaluated by panelists). These results indicate that meat quality traits in terms of phenotypic correlations with color indices are not related, which is in conformance with findings of the current study.

In a study by Wulf et al. (1997) on multi-breed beef cattle in USA, after 27 hours post-mortem for color measurements and 14 days post-mortem for panel evaluations, phenotypic correlations between sensory and color measurements were reported. Their results indicated weak correlations of tenderness, juiciness, flavor with L* (0.34, 0.1, and 0.02, respectively), a* (0.21, 0.1, and -0.09, respectively) and b* (0.37, 0.2 and -0.3, respectively) values. The results from this study also confirm our findings.

Overall, the traits of interest in this study were not phenotypically speaking strongly correlated, despite our findings about some strong genetic correlations (see part 3.4.3). Still these results are useful to predict the changes in color overtime. For example, by measuring color at day 3 post-mortem we would have knowledge that how it is associated with color at day 29 post-mortem. The phenotypic correlation estimates between meat color and sensory taste panel attributes did not show strong associations between them. The reason for differences from our results and other studies might be due to differences in breeds as well as in post-mortem aging.

3.4.2. Heritability estimates:

One of the most important traits, which helps consumers to choose an animal protein, is the color of fresh meat. As a matter of fact consumers use discoloration of the meat product as an sign for freshness of the meat (Mancini & Hunt, 2005). Color of the meat arises from heme containing protein, Myoglobin. Progress in color stability and economic improvements in this regard can be achieved through our knowledge of properties of this molecule, which can be measured objectively with different color indices (L* for lightness of the meat, a* for red to green value, and b* for blue to yellow) in meat products. For better understanding of color measurements, these indices can be converted to Chroma (saturation of the color) and Hue (color of the meat). One important property of traits in relation to improving beef quality is heritability. Heritability is a measure of the degree of phenotypic variation in traits that is because of the genetic variation in a population. With knowledge of the extent of inheritance of these traits, animal scientists can work on using genetic selection to improve meat color as well as its stability for next generations.

Our results indicated that lightness and Hue are moderately to highly heritable at days 3 and 29 post-mortem. The heritability estimates for retail colour indices after days 0, 2 and 4 days of shelf life showed they have negligible heritability.

In a study on adapted and temperate beef cattle breeds, both Johnston et al. (2003) and Reverter et al. (2003) reported a heritability of 0.18 and 0.17 respectively, for lightness of the meat. The estimates of heritability from both of these studies are lower than our estimate of heritability for lightness. Wolcott et al. (2009) in a study on beef populations in northern Australia, after 20-24 hours post-mortem reported heritability for lightness of the meat as 0.42. This result is in accordance with our heritability estimate of lightness at day 3 post-mortem (0.49). Another study by Aass (1996) on Norwegian cattle indicated a heritability of 0.30 for lightness which was lower than our estimate. In another study on Nellore cattle in Brazil, Marín-Garzón et al. (2019) reported a similar heritability estimate for lightness of the meat (0.48) in a single trait analysis. Our heritability estimate in this study for lightness at day 3 post-mortem was 0.49, which was in the range of their report.

Savoia et al. (2019) in their study on 115 herds of Piemontese bulls in Italy, used 7 days of aging post-mortem and estimated the intra-herd heritability for lightness (0.30), Chroma (0.13) and Hue (0.13) of the meat. Their results were lower for lightness (0.48), in the range for Chroma (016) and lower for Hue (0.58) after 3 days of aging, than the estimates of current study.

Lambe and Simm (2014) indicated that heritability estimates for color indices across species for lean color is low to moderate (ranging from 0.25 to 0.50) and for myoglobin content is moderate to high (0.50 to 1.00). The ranges that they reported in their study are in conformance with our results as our findings suggested that color indices such as lightness and Hue are moderately heritable after 3- and 29-days post-mortem, while on the other hand Chroma has a low heritability.

Boukha et al. (2007) in a study on Piemontese beef cattle reported heritability estimates for lightness (0.22), Chroma (0.16) and Hue (0.49) after 8 days post-mortem. These results are in conformance with our findings for Chroma and Hue but were lower than our estimate for lightness at day 3 post-mortem. In another study on Piemontese beef cattle, Cecchinato et al.

(2009) reported heritability estimates for lightness (0.31) and Hue (0.63) which was lower and in the range of our estimates at day 3 post-mortem.

Cecchi et al. (2004) studied the genetic variability of meat attributes in three different muscles (including *Longissimus dorsi*) in Chianina beef cattle breed. The measurements took place before and after 48 hours storage. Heritability were estimated for lightness (0.02 before storage and 0.03 48 hours after), Chroma (0.00 before storage and 0.03 48 hours after) and for Hue (0.05 before storage and 0.12 48 hours after) measured in *Longissimus dorsi*. These findings with retail color results from current study are in conformance, indicating that retail color traits are lowly heritable across distinct cattle populations and breeds.

In a study on stability of beef color in seven most famous breeds in USA, (including Angus, Hereford, Red-Angus, Limousin, Gelbvieh, Charolais and Simmental), King et al. (2010) reported heritability estimates for some color indices on day 0 and 6 of display. They reported heritability estimates at days 0 and 6 for lightness (0.24 and 0.40, respectively), and Chroma (0.00 and 0.13, respectively). Comparing these results to our findings for retail traits, lightness (h^2= 0.01 at day 0, h^2= 0.07 at day 2, and h^2= 0.04 at day 4) was much higher than our estimates, and Chroma (h^2= 0.03 at day 0, h^2= 0.03 at day 2, and h^2= 0.04 at day 4) was in the range for both day 0 and 2, and higher at day 4 of the shelf life. In addition, these researchers reported heritability estimates for a* (h^2= 0.06 at day 0, and h^2= 0.14 at day 6) and b* (h^2= 0.00 at day 0, and h^2= 0.13 at day 6) as well. These estimates did not show a high heritability and can be indirectly compared to our estimates of Chroma and Hue (0.07 at day 0, 0.05 at day 2, and 0.02 at day 4) which were in the range with what was reported in their study.

Overall, our heritability estimates of color indices after 3- and 29-days post-mortem in many cases were in the range and some differences could be seen among the cited studies. Our findings suggested that lightness and Hue have moderate to high heritability depending on how many days aged post-mortem. This means that we can improve the stability of these two color indices by genetic selection based on individual merit through generations.

Low heritability estimates for different retail shelf life days of the current study suggests that there are no significant opportunities for genetic improving of these traits. In other words, with controlling environmental factors, there are more opportunities to improve stability of color indices in different display days.

The reason for some differences between our estimates and other studies could be originated from different populations, and population specific features (such as allele frequencies) as well as different aging periods post-mortem and under different studies.

3.4.3. Genetic correlations:

Meat color, as has been mentioned before, is one of the critical traits that affects consumer's choice when purchasing a meat product. Looking at the relationship between meat color and palatability traits often low correlations can be found and nevertheless, customers use color of the meat for acceptance or rejection of a product (Hood and Riordan 1973). Considering this important fact, in the present study we estimated genetic correlations between sensory taste panel traits and color indices (L*, Chroma and Hue). By estimating these genetic correlations, which are due to common genetic causes between these traits, there is an opportunity for improvement in meat quality attributes with developing prediction models as well as selection index equations. Moreover, the genetic correlation information can be used as precursors of understanding the relationship between sensory and color indices in different post-mortem aging, as well as improving the visual color of the products and in future maybe opens a door for possibility of replacing the sensory taste panel traits by non-invasive, cheap, and easy to apply color measurements. Furthermore, this information will enhance our knowledge of biological background and their relationship together for these traits.

Johnston et al. (2003) an and Reverter et al. (2003) studied the genetic and phenotypic characterization of temperate and adapted breeds in Australia and they reported genetic correlation between lightness and tenderness values ranging from 0.03 to 0.40. Their result was in conformance with our findings, where we estimated weak genetic correlations between lightness and tenderness at both days 3 and 29 post-mortem.

Cecchi et al. (2004) in a study on Chianina breed in three different muscles before and 48 hours after storage reported the genetic correlations between color indices traits. As their results indicated, in *Longissimus dorsi*, lightness before and after storage had a strong correlation (> 0.7). In addition, they reported a moderate genetic correlation in Chroma as well as a weak correlation for Hue before and after storage. Their results regarding lightness were in conformance with our findings (the strong genetic correlation for this trait between day 3 and 29 post-mortem) while for Chroma and Hue their estimates were different. These researchers also reported significant correlations between tenderness (measured by WBSF) and Chroma (48 hours after storage), and with redness of the meat (a* before and after storage) in a different muscle (triceps brachii muscle). These results are in agreement with the relationship between color indices and sensory traits that we found in this study (such as correlations between sensory connective tissue, overall tenderness and Chroma).

Wulf et al. (1996) studied beef palatability attributes of Charolais and Limousin sired beef as continental European breeds. They reported that lean color has a significant effect on meat tenderness, and darker color meat had higher values of shear force (less tender) and less tenderness score by panelists. These researchers also indicated that with different post-mortem aging, they observed changes in color attributes and the interaction between color and post-mortem aging was in fact significant. In addition, they stated that normal color meat had higher scores for beef flavor intensity comparing to dark or pale lean beef. Furthermore, their study showed, lean color and panel juiciness were not related. The results from genetic correlations between color indices and sensory attributes are confirming the relationship between Chroma (saturation index for color of the meat) and overall tenderness, connective tissue, flavor intensity and off-flavor in different post-mortem aging days. Accordingly, we did not find any relationship between color and panel juiciness with genetic correlations lower than 0.1.

Gagaoua et al. (2020) in a review on protein biomarkers of meat color in beef reported that tenderness and color indices have common pathways and putative protein biomarkers indicating that these two important traits are genetically associated. Examples of common biological pathways are proteolysis pathways, and catalytic pathways (which includes different sub-pathways including glycolysis). As common biomarkers they found the HSPs (Heat Shock Proteins). It has been reported that HSPs gene family is involved in apoptosis regulation and conversion of muscle to meat and thus they can affect meat palatability attributes. On the other hand, the same genes were associated with beef color. Interestingly, in the present study we found strong genetic correlations between Chroma index (day 3) with connective tissue (day 3), and Chroma (day 29) with overall palatability and off-flavour (day 29), along with some moderate genetic correlations between Chroma (day 3) with overall tenderness and flavor intensity (day 3). The relationship between pigmentation and Chroma index in muscle and connective tissue as well as other palatability attributes might be due to breed effect, muscle fiber type and physical activity of animals (Mancini & Hunt, 2005). Mancini & Hunt (2005) stated that increased muscle activity will affect the enzymatic profile in the muscle, hence different types of muscle fiber populations can be observed which per se affects palatability attributes and the way light is absorb and reflected influencing meat color attributes.

In general, these correlations are confirming that color traits and sensory attributes are genetically associated as the mentioned review revealed common pathways and putative protein biomarkers between meat color and sensory taste panel traits.

Having control over beef quality (such as sensory and color attributes) are important to comply with both customers and producers' interests. There are many genetic and environmental factors controlling the variation in meat quality traits, and this is the reason why many studies are conducted in order to understand the nature of these traits, factors affecting them and their relationships. Genetic correlation estimations of the current study are presenting biological relationship between color and sensory traits during different post-mortem aging. The results from our study indicated that color indices such as Lightness and Chroma are genetically correlated to sensory tenderness, flavor, and overall palatability. To the knowledge of the author, there are not many reports looking into genetic correlation of these indices and sensory traits in beef. These genetic correlations will help producers to have a better understanding of the relationship of these traits, so they would know selection for one trait how much and in which direction will change other economically important traits.

3.4.4. Retail traits trend analysis:

In recent years the meat industry has been trying to adapt to market demands and customer preferences. Retail display of the product, especially color, have crucial role in customer's perception of the product (Feldhusen, Warnatz, Erdmann, & Wenzel, 1995). While storing the product in retail display, several changes will occur in the meat, which can affect its quality (Ferguson et al., 2001). These changes can affect meat's sensory attributes (such as tenderness, flavor, and juiciness) as well as color of the product. During storage of the meat, myoglobin's oxygenation/oxidation will influence its color (Mancini & Hunt, 2005). However, to enhance sensory attributes of the product there is a need to manipulate the product prior to presenting to the market. Hence, it is imperative to have knowledge of these changes for a better understanding of retail shelf life, and ultimately predicting these changes (Delmore, 2007; Taoukis & Labuza, 1989) . It has been reported that color measurements on different display days are very repeatable and hence there are good indices for studying these economic traits under different conditions (King, Shackelford, Kalchayanand, & Wheeler, 2012). The current study was carried out in order to understand the changes of color in commercial crossbred cattle in western Canada, and to identify if these changes are significant during three different time points (day 0, 2 and 4) of retail display days.

King et al. (2011) in a study on seven major beef breeds in USA, after 18 days post-mortem aging, measured color indices in 6 different retail display days (from day 0 to day 6). These researchers reported that lightness of the meat did not significantly change between days 0 to 2, but there was significant decrease between day 0 and 4, and day 2 and 4. These results are in conformance with our findings, where we observed significant decrease in lightness of the meat between day 0 and 4 as well as day 2 to 4 of shelf life. They also stated that Chroma index significantly reduced between days 0 to 2, 2 to 4, and 0 to 4 of shelf life. Comparing to our results, we did not find any significant decrease from day 0 to 2 but in conformance with their findings, Chroma index decline was significant between day 2 to 4, and 0 to 4 of display life. In addition, according to their study, there were significant decline in Hue between days 0 to 2 but the differences between day 0 to 4, and day 2 to 4 of shelf life, were not significant. These findings are different from the current study, as we found significant decrease in Hue index between day 2 to 4 and, 0 to 4 of retail display.

In another study on commercial carcasses in USA, after 14 and 35 days of aging post-mortem, researchers evaluated the color changes and color stability of lean in beef during days 0, 1, 4, 7 and 11 of display life (King et al., 2012). They reported that lightness of the meat decreased considerably at first 4 days of shelf life and after that, the changes were negligible. These findings are in conformance with our results. In addition, they found no changes in Hue index in the first 7 days of display, which is different from our findings where Hue index decreased from day 0 to 4, and there was significant decrease between days 0 to 4, and 2 to 4. Lastly, they reported Chroma values went down during display days and this decline was more rapid between days 4 to 7. These results are in agreement with our findings regarding the observed decrease in Chroma index between days 0 to 4 of shelf life.

In a study with 16 low grade USDA beef *Longissimus lumborum* steaks from a commercial harvest facility, after aging 45 days post-mortem, and 7 days of retail display, Ribeiro et al. (2020) reported color measurements from their samples. As their results indicated, lightness was significantly lower in day 2 comparing to day 0, as well as significant decline between day 0 and 4. However, the authors did not observe any significant changes between day 2 and 4 of display. In addition, these researchers reported the changes in a* and b* color indices as well. They stated that a* was significantly lower between day 0 and 2, and 0 and 4 of shelf life, while for b* the decline was significant in each day. These results are in partial agreement with our findings regarding significant differences between day 0 and 4, as well as 0 and 2 for lightness, Chroma and Hue.

Previous studies on regression trajectory regarding color changes stated that increased aging days at retail display considerably affects the color of the meat. This also has been shown to be associated with metmyoglobin build up and accumulation in beef. Past studies showed that display color measurements are repeatable, and variations between animals are consistent, but prolonged retail display days have an extensive impact on color of the product (King et al. 2012, Hood 1980 and Olivera et al. 2013). Our findings are in agreement with the fact that increased retail shelf life will decrease color quality of the meat.

In general, the interest of this study was to investigate changes in color indices in different retail display life, and understand if these differences are significant or not, thus we could suggest a possible optimum day for shelf life before color changes become too apparent. Different studies had different optimum days of shelf life suggested, which can be due to the fact that they have undergone different aging periods, the longer this period was, the possibility of developing rancidity and off-flavor properties would be increased which will have a negative effect on the display life of the product afterwards. As per our findings, the optimum day for product retail display is 2 days and after that color changes will be more obvious, and the product could be discriminated against by customers.

3.5. Conclusion

Our results indicate that lightness and Hue are two color indices that have high phenotypic and genetic correlations between day 3 and 29 post-mortem. This high correlation estimated for each trait with itself shows that by measuring them once at day 3 post-mortem, we can predict color indices after 29 days aging post-mortem. Most of the Pearson phenotypic correlations found in this study between color and palatability traits at day 3 and 29 post-mortem were weak and are therefore of little practical use for the overall aim of this study.

The heritability estimates from this study showed that lightness and Hue indices had moderate to high heritability. However, the estimates for Chroma and for color indices after 0, 2 and 4 days of retail display were of low magnitude. The low estimates for these traits indicate that there are few genes with additive effect influencing the expression of these traits, and they are mostly affected by environmental factors. Thus, the direct selection on these traits will not generate a considerable genetic improvement. For these traits, management of environmental factors would be the best option for maintaining meat colour quality during retail of the product.

Our results indicate that lightness and Hue are two color indices that have high phenotypic and genetic correlations between day 3 and 29 post-mortem. Thus, we conclude that it is possible to predict color indices after 29 days aging post-mortem by measuring the target traits once at day 3 post-mortem. Moreover, the genetic correlation results from this study showed that Chroma and panel connective tissue as well as Chroma with overall palatability and off-flavor are highly correlated. These strong genetic correlations indicate that these traits are simultaneously influenced by genes with additive effect and molecular pathways, thus including direct selection for Chroma will lead to corresponding genetic improvement in palatability attributes. In addition, these results can be used for a better understanding of associations between these traits, and potentially for prediction models in further analysis if a selection index equation is developed aiming to improve meat quality attributes by including color variables.

Lastly, trend analysis for retail color indices showed that all three measured colors (L*, Hue and Chroma) have been significantly decreased from day 2 to 4 as well as 0 to 4 of shelf life. These results suggested that the best time for retail display is from day 0 to 2 and after that due to significant decline in color quality; the product might be discriminated against.

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Table 3.1 Descriptive statistics of color traits (L*, Hue and Chroma) on day 3 and 29 post-mortem, Traits, abbreviations, number of animals (N), phenotypic mean, standard deviation (SD), Minimum value (Min), Maximum value (Max), Coefficient of variation (CV).

Traits	**N**	**Mean**	**SD**	**Min**	**Max**	**CV%**
Lightness of the meat, day 3	1,147	37.12	2.65	29.97	44.44	7
Chroma saturation index of color, day 3	1,146	22.11	1.77	17.17	27.02	8
Color of the meat, hue angel, day 3	1,137	34.66	1.99	29.82	39.85	5
Lightness of the meat, day 29	1,155	38.83	2.81	31.04	46.53	7
Chroma saturation index of color, day 29	1,164	17.72	2.34	11.24	24.12	13
Color of the meat, hue angel, day 29	1,163	40.66	4.28	30.23	53.29	10

Number of animals (N), phenotypic mean, standard deviation (SD), Minimum value (Min), Maximum value (Max), Coefficient of variation (CV).

Table 3. 2 Descriptive statistics of retail traits (L*, Hue and Chroma) on different shelf life days (0, 2 and 4), number of animals (N), phenotypic mean, standard deviation (SD), Minimum value (Min), Maximum value (Max), Coefficient of variation (CV).

Traits	N	Mean	SD	Min	Max	CV%
Lightness of the meat, Shelf life 0 days	1,299	40.10	2.44	33.55	46.58	6
Chroma saturation index of color, Shelf life 0 days	1,311	23.16	2.34	16.49	29.82	10
Color of the meat hue angel, Shelf life 0 days	1,318	34.57	2.14	28.72	40.41	6
Lightness of the meat, Shelf life 2 days	1,232	39.92	2.50	33.17	46.36	6
Chroma saturation index of color, Shelf life 2 days	1,240	23.33	2.12	17.45	29.16	9
Color of the meat, hue angel, Shelf life 2 days	1,235	35.54	2.01	30.18	40.99	5
Lightness of the meat, Shelf life 4 days	1,195	39.67	2.58	33.06	46.73	6
Chroma saturation index of color, Shelf life 4 days	1,212	22.17	2.57	14.97	28.99	11
Color of the meat, hue angel, Shelf life 4 days	1,174	36.83	2.35	30.68	43.49	6

Number of animals (N), phenotypic mean, standard deviation (SD), Minimum value (Min), Maximum value (Max), Coefficient of variation (CV).

Table 3. 3 Phenotype Pearson correlations (*r*) and their standard errors between day 3 and day 29 of each color trait

Trait	***r* ± SE**	**p-value**
Lightness of the meat	0.61 ± 0.01	0.00
Chroma saturation index of color	-0.01 ± 0.02	0.63
Color of the meat, hue angel	0.53 ± 0.02	0.00

Table 3. 4 Pearson's correlation coefficient between meat color and sensory taste panel traits measured at days 3 and 29 post-mortem.

Traits[1]	OT 3	OP 3	CT 3	FI 3	OF 3	SJ 3	OT 29	OP 29	CT 29	FI 29	OF 29	SJ 29
COLOR_L_3	0.19 ± 0.02	0.05 ± 0.03	0.27 ± 0.02	-0.006 ± 0.02	-0.09 ± 0.02	-0.05 ± 0.02	0.22 ± 0.02	0.03 ± 0.02	0.17 ± 0.02	0.01 ± 0.02	0.01 ± 0.02	0.05 ± 0.02
COLOR_CH_3	0.29 ± 0.02	0.22 ± 0.02	0.16 ± 0.02	0.04 ± 0.02	0.05 ± 0.02	0.05 ± 0.02	0.20 ± 0.02	0.03 ± 0.02	0.11 ± 0.02	-0.002 ± 0.02	0.02 ± 0.02	-3e-04 ± 0.02
COLOR_HU_3	0.13 ± 0.02	0.06 ± 0.03	0.18 ± 0.02	0.03 ± 0.02	-0.06 ± 0.02	-0.02 ± 0.02	0.17 ± 0.02	0.07 ± 0.02	0.16 ± 0.02	0.06 ± 0.02	0.05 ± 0.02	0.01 ± 0.03
COLOR_L_29	0.15 ± 0.02	0.04 ± 0.02	0.21 ± 0.02	-0.02 ± 0.02	-0.08 ± 0.02	-0.09 ± 0.02	0.19 ± 0.02	0.07 ± 0.02	0.13 ± 0.02	0.02 ± 0.02	0.07 ± 0.02	0.02 ± 0.02
COLOR_CH_29	-0.07 ± 0.02	-0.07 ± 0.02	-0.05 ± 0.02	-0.11 ± 0.02	0.05 ± 0.02	-0.07 ± 0.02	-0.06 ± 0.02	-0.10 ± 0.02	-0.01 ± 0.02	-0.17 ± 0.02	-0.09 ± 0.02	-0.08 ± 0.02
COLOR_HU_29	0.15 ± 0.02	0.10 ± 0.02	0.17 ± 0.02	0.10 ± 0.02	-0.07 ± 0.02	0.01 ± 0.02	0.18 ± 0.02	0.15 ± 0.02	0.11 ± 0.02	0.18 ± 0.02	0.12 ± 0.02	0.08 ± 0.02

[1] OT= overall tenderness; OP= overall palatability; CT= connective tissue; FI= flavor Intensity; OF= off-flavour; SJ= sustain juiciness; COLOR_L: Lightness of the meat; COLOR_CH: Chroma saturation index of color; COLOR_HU: Color of the meat, hue angel; Days 3 and 29 post-mortem.

Table 3. 5 Genetic parameter estimations and their standard errors for color traits day 3 and 29 post-mortem

Trait	$\sigma_a^2 \pm$ SE	$\sigma_e^2 \pm$ SE	$h^2 \pm$ SE
Lightness of the meat, day 3	2.447 ± 0.450	2.529 ± 0.348	0.491 ± 0.077
Chroma saturation index of color, day 3	0.446 ± 0.168	2.283 ± 0.173	0.163 ± 0.059
Color of the meat, hue angel, day 3	1.711 ± 0.269	1.231 ± 0.197	0.581 ± 0.074
Lightness of the meat, day 29	1.576 ± 0.443	4.107 ± 0.398	0.277 ± 0.073
Chroma saturation index of color, day 29	0.279 ± 0.181	2.842 ± 0.201	0.089 ± 0.057
Color of the meat, hue angel, day 29	3.921 ± 0.912	7.412 ± 0.779	0.346 ± 0.073

σ_a^2= Additive genetic variance; σ_e^2= Residual variance; h^2= heritability; SE= Standard error

Table 3. 6 Genetic parameter estimations and their standard errors for retail traits on 0, 2 and 4 days of shelf life

Trait	$\sigma_a^2 \pm$ SE	$\sigma_e^2 \pm$ SE	$h^2 \pm$ SE
Lightness of the meat, Shelf life 0 days	0.064 ± 0.207	4.312 ± 0.275	0.014 ± 0.047
Chroma saturation index of color, Shelf life 0 days	0.120 ± 0.159	3.228 ± 0.205	0.036 ± 0.047
Color of the meat hue angel, Shelf life 0 days	0.226 ± 0.161	2.706 ± 0.187	0.077 ± 0.054
Lightness of the meat, Shelf life 2 days	0.379 ± 0.290	4.510 ± 0.333	0.077 ± 0.058
Chroma saturation index of color, Shelf life 2 days	0.101 ± 0.161	3.184 ± 0.209	0.030 ± 0.049
Color of the meat hue angel, Shelf life 2days	0.156 ± 0.166	2.950 ± 0.204	0.050 ± 0.053
Lightness of the meat, Shelf life 4 days	0.234 ± 0.302	5.138 ± 0.369	0.043 ± 0.056
Chroma saturation index of color, Shelf life 4 days	0.259 ± 0.252	5.092 ± 0.331	0.048 ± 0.047
Color of the meat hue angel, Shelf life 4 days	0.109 ± 0.227	4.529 ± 0.303	0.023 ± 0.049

σ_a^2= Additive genetic variance; σ_e^2= Residual variance; h^2= heritability; SE= Standard error

Table 3. 7 Genetic correlations and their standard errors between day 3 and day 29 of each trait

Trait	Genetic correlation ± SE
Lightness of the meat	1.03 ± 0.04
Chroma saturation index of color	-0.87 ± 0.55
Color of the meat hue angel	0.79 ± 0.08

Table 3. 8 Genetic correlations estimates and their standard error between color traits and sensory traits and on day 3 and day 29 post-mortem

Traits[1]	OT 3	OP 3	CT 3	FI 3	OF 3	SJ 3	OT 29	OP 29	CT 29	FI 29	OF 29	SJ 29
COLOR_L_3	0.21 ± 0.14	0.03 ± 0.16	0.45 ± 0.18	-0.08 ± 0.19	0.02 ± 0.19	0.09 ± 0.29	0.32 ± 0.15	0.08 ± 0.22	0.10 ± 0.23	0.17 ± 0.21	0.03 ± 0.24	0.21 ± 0.26
COLOR_CH_3	0.57 ± 0.19	0.18 ± 0.22	0.75 ± 0.31	0.42 ± 0.28	0.32 ± 0.27	-0.06 ± 0.40	0.38 ± 0.2	-0.08 ± 0.3	0.07 ± 0.32	0.15 ± 0.30	0.01 ± 0.33	0.005 ± 0.36
COLOR_HU_3	0.03 ± 0.14	-0.04 ± 0.15	0.13 ± 0.19	-0.14 ± 0.18	-0.07 ± 0.18	0.09 ± 0.28	0.24 ± 0.15	0.06 ± 0.20	0.002 ± 0.21	0.19 ± 0.20	0.12 ± 0.22	0.13 ± 0.25
COLOR_L_29	-0.04 ± 0.19	-0.05 ± 0.20	0.27 ± 0.23	-0.03 ± 0.23	-0.24 ± 0.23	0.17 ± 0.35	0.14 ± 0.20	0.08 ± 0.26	0.21 ± 0.27	0.25 ± 0.26	-0.04 ± 0.29	-0.21 ± 0.31
COLOR_CH_29	0.20 ± 0.27	0.53 ± 0.28	-0.09 ± 0.39	0.31 ± 0.31	0.54 ± 0.30	1.34 ± 0.37	0.07 ± 0.31	0.69 ± 0.37	-0.36 ± 0.44	0.06 ± 0.39	0.87 ± 0.43	0.50 ± 0.48
COLOR_HU_29	0.01 ± 0.16	-0.15 ± 0.18	0.15 ± 0.22	-0.15 ± 0.20	-0.44 ± 0.20	-0.39 ± 0.35	0.01 ± 0.19	-0.17 ± 0.24	0.28 ± 0.25	0.22 ± 0.24	-0.37 ± 0.27	-0.22 ± 0.28

[1] OT= overall tenderness; OP= overall palatability; CT= connective tissue; FI= flavor Intensity; OF= off-flavour; SJ= sustain juiciness; COLOR_L: Lightness of the meat; COLOR_CH: Chroma saturation index of color; COLOR_HU: Color of the meat hue angel; Days 3 and 29 post-mortem.

Figure 3. 1 Changes in L* along time (day 0, 2 and 4 shelf life days)

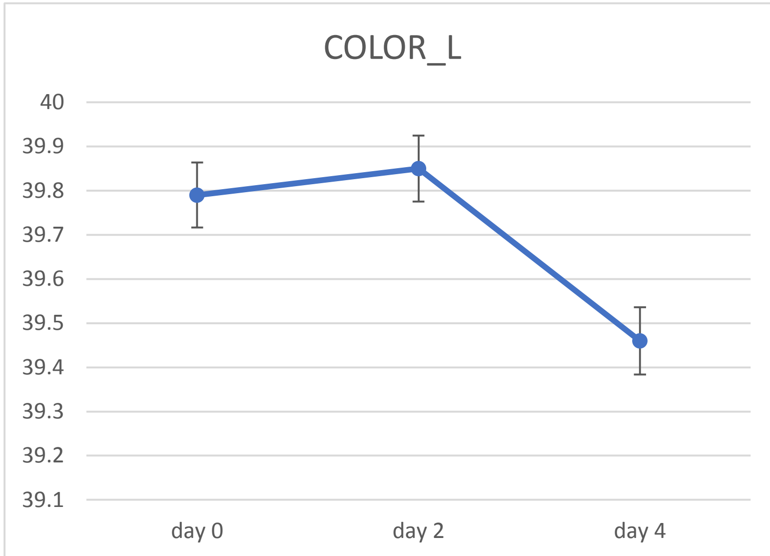

Table 3. 9 Significant differences between different shelf life days for lightness of the meat

Differences between days	p-Value
0-2	0.7188
0-4	<.0001
2-4	<.0001

Figure 3. 2 Changes in Chroma along time (day 0, 2 and 4 shelf life days)

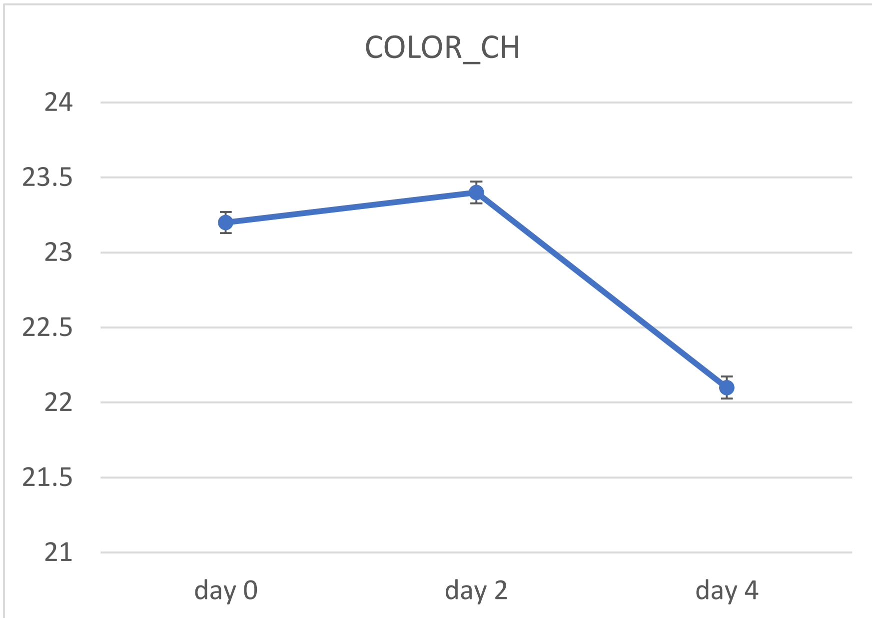

Table 3. 10 Significant differences between different shelf life days for Chroma index in meat

Differences between days	p-Value
0-2	0.033
0-4	<.0001
2-4	<.0001

Figure 3. 3 Changes in Hue along time (day 0, 2 and 4 shelf life days)

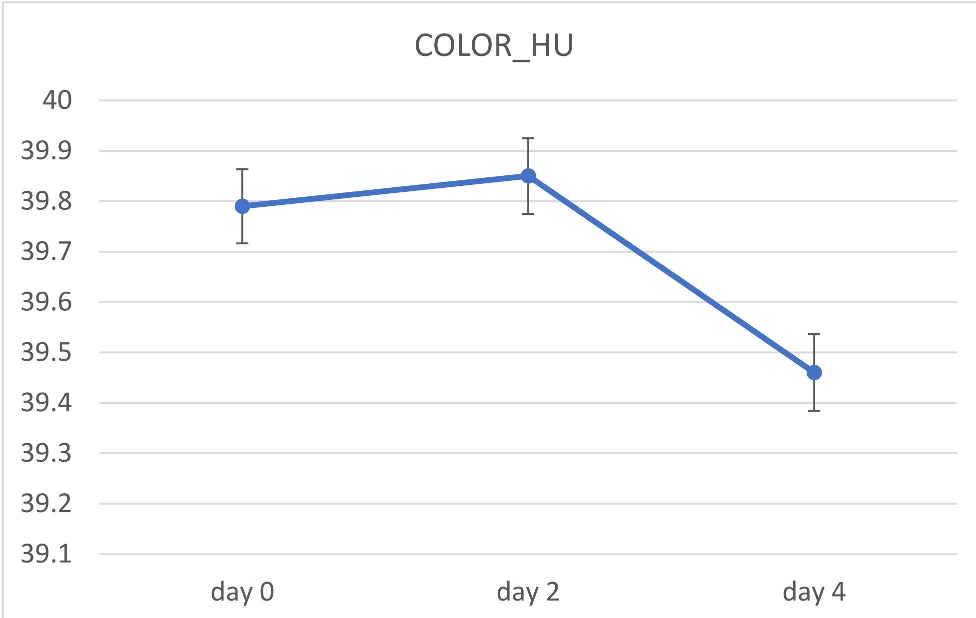

Table 3. 11 Significant differences between different shelf life days for Hue index of the meat

Differences between days	p-Value
0-2	0.7188
0-4	<.0001
2-4	<.0001

Chapter 4. Prediction models for estimating meat sensory attributes from objectively measured traits on days 3 and 29 post-mortem

4.1. Introduction

Sensory attributes of beef meat quality are contributing factors in consumer's satisfaction. It has been reported these attributes are variable which leads to consumer's dissatisfaction of a product. In recent years consumer's preference regarding beef consumption, more and more shifted towards sustainable farming with high quality, safe and nutritious products. Between mentioned criteria, quality attributes play a major role in consumer satisfaction of a product, and determines consumer choice of purchase in the future (Grunert et al., 2004). Previous studies indicated that amongst beef quality attributes, tenderness and flavor are most important factors which affects the overall liking of the meat (Henchion, McCarthy, Resconi, & Troy, 2014; Miller et al., 2001; Troy & Kerry, 2010).

On the other hand, for consumer's guaranteed choice of purchase of a product meat consistency is reported to be as important (McCarthy et al., 2017). Achieving a high quality and consistent beef meat product is challenging, as changes in beef is dynamic regarding its biochemical properties and is subjected to variation. These variations can originate from range of intrinsic as well as extrinsic factors, namely factors from farm such as rearing conditions, slaughterhouse circumstances, muscle to meat transformation and characteristics, and other contributing factors such as animal sex, breed, and muscle type (Maltin et al., 2003; Ferguson et al., 2001; Gagaoua et al., 2018, 2019).

In order for industry to remain competitive and satisfy consumer's demands in the market, it is very important to be able to predict these eating quality aspects at the consumer level (Hocquette et al., 2014). Beef industry works towards predicting quality attributes using these intrinsic and extrinsic factors to expand and develop modeling tools. The ultimate goal of using these tools are to predict and provide consistent products, which meets consumer's preference specifically regarding sensory attributes (Gagaoua et al., 2019). These modeling tools can predict meat quality at different points throughout the supply chain. Waltemath et al. (2011) defined modeling as a mathematical approach for manipulation of a biological system, which in this context sensory attributes are biological traits that we aim to predict and manipulate. To accurately predict sensory traits, which are complex with multidimensional variables, we need to identify other traits and variables related to sensory attributes and integrate them into a sophisticated model with several criteria (Bouyssou et al., 2000). For this purpose, we need to identify both criteria (the quality traits that we want to improve) and indicators (for example objective measurements to be used for prediction of subjective measured traits) leading to an integration of these criteria to form a prediction model equation (Hocquette et al., 2012).

Sensory quality attributes are good indicators of consumer acceptance of a product, but the downside is that they are hard to measure, time consuming and labor intensive. While objectively measured traits such as WBSF are relatively cheap, they are simplistic and one-dimensional which cannot completely describe consumer's preference of a product (Watson et al., 2008). Perry et al. (2001) showed that WBSF as an objective measurement is not a good indicator for sensory attributes such as tenderness or juiciness as it does not account for all the aspects that the consumers perceive while using a product.

With developing an accurate prediction model for sensory attributes from objective measured traits besides incorporating as much as other contributing factors (environmental and intrinsic), we might be able to predict sensory attributes in beef meat at different post-mortem aging periods.

Therefore, in this chapter we used our existing data to develop a prediction model for sensory attributes. For this purpose, we hypothesised that:

4.1.1 Hypotheses:

1. Sensory traits at day 3 post-mortem can be predicted from objectively measured traits at day 3 post-mortem.
2. Sensory attributes at day 29 post-mortem can be predicted from objectively measured traits at day 29 post-mortem.
3. Sensory traits at day 29 post-mortem can be predicted from objectively measured traits at day 3 post-mortem.

4.1.2. Objectives:

The objective of this study is to determine if meat quality attributes measured by WBSF, fat content, pH and color indices can be used to predict sensory trait attributes measured at day 3 and 29 post-mortem.

4.2. Materials and methods:

After arranging the data, outlier detection and performing different analysis on them (see chapter 2 and 3), we decided to explore more and see if we can use these existing data to develop a prediction model for sensory attributes in different post-mortem aging days.

In order to develop an accurate model, we used objectively measured traits including WBSF, fat content, pH and color indices (Hue and Chroma) for our analysis. In this study, we excluded lightness values as it was highly genetically correlated to Hue (0.87), and we chose to keep Hue in our model as it has a higher heritability estimate (0.58, see chapter 2). The same fixed effects previously described were included in the model. These effects were as follows: slaughter age, contemporary grouping, animal sex, and British and Continental breed fractions. A linear regression model was implemented for sensory attributes, as follow:

$$\boldsymbol{Y_{ij} = WBSF_i + Fat_i + pH_i + Chroma_i + Hue_i + Slau\,age_i + CG_i + Sex_i + BC_i + e_{ij}}$$

Where $\boldsymbol{Y_{ij}}$ is our sensory traits; $\boldsymbol{Slau\,age_i}$ is age at the slaughter; $\boldsymbol{CG_i}$ is the contemporary grouping; $\boldsymbol{BC_i}$ is breed composition (British and Continental); $\boldsymbol{Sex_i}$is the sex of the animal; and $\boldsymbol{e_{ij}}$ is residual effects that are included in the model.

This model was used to predict sensory attributes (overall tenderness, overall palatability, flavor intensity, off-flavor, sustained juiciness and connective tissue) measured at day 3 and 29 from objectively measured traits at day different post-mortem time points.

4.3. Results

The results of prediction model analysis for sensory attributes at day 3 post-mortem from objectively measured traits at day 3 post-mortem are presented in Table 4.1. These results indicated that at day 3 post-mortem, between objectively measured traits WBSF and fat content were significant for all sensory attributes while meat pH was only significant for sensory off-flavor. In addition, Chroma was significant for overall tenderness, overall palatability and connective tissue while Hue was only significant for connective tissue and sustained juiciness. The highest model R-squared values were identified for overall tenderness (0.48), overall palatability (0.36) and connective tissue (0.34).

The results for prediction of sensory eating quality traits at day 29 post-mortem using objectively measured traits at day 29 post-mortem are presented in Table 4.2. These results also indicated that WBSF and fat content were significant for all sensory attributes under this study. In addition, meat pH was found to be significant for overall tenderness, overall palatability, connective tissue and sustained juiciness. Chroma index was significant for overall palatability, sustained juiciness, flavor intensity and off-flavor while Hue was only significant in overall tenderness and connective tissue. The highest R-squared for the prediction models of objectively measured traits at day 29 post-mortem obtained were for overall tenderness (0.39) and overall palatability (0.25).

Finally, Table 4.3 presents the results of sensory prediction at day 29 post-mortem using objectively measured traits at day 3 post-mortem. These results indicated that WBSF and fat content at day 3 post-mortem were significant for all sensory attributes at day 29 post-mortem, except that fat content was not significant for connective tissue. Meat pH measured at day 3 was only significant for overall palatability, flavor intensity and off-flavor at day 29 post-mortem. Both Chroma and Hue were significant for overall tenderness and connective tissue, while for flavor intensity only Chroma, and for sustained juiciness only Hue were significant. The highest model R-squared obtained from these analyzes were for overall tenderness (0.39) and overall palatability (0.23).

Our findings suggested that contemporary grouping is significant for all of our prediction models in different post-mortem aging periods (day 3 and 29 post-mortem). While animal sex was only significant for sensory overall tenderness and connective tissue in all prediction models in this study. At day 3 post-mortem, we can see that pH was only significant for off-flavor while it was mostly significant for all sensory attributes except flavor intensity at day 29 post-mortem. In addition to that, meat pH was only significant for flavor intensity, off-flavor and overall palatability when predicting sensory at day 29 from objectively measured traits at day 3 post-mortem. Color attributes, Chroma and Hue were significant in different days for different traits.

At day 3 post-mortem, Chroma was significant for overall tenderness, overall palatability, and connective tissue and at day 29 it was significant for overall palatability, sustained juiciness, flavor intensity and off-flavor. Hue on the other hand, at day 3 post-mortem was significant for connective tissue, sustained juiciness, and off-flavor and at day 29 found significant for overall tenderness and connective tissue. While predicting sensory attributes at day 29 form objective measurements at day 3, Chroma was significant for overall tenderness, connective tissue and off-flavor, and Hue was significant for overall tenderness, sustained juiciness, and connective tissue.

4.4. Discussion

Juárez et al. (2012) in their research on quantifying factors influencing meat texture on 112 steers from four crossbreeds, reported the possibility of capturing more than 70% of tenderness variation by incorporating many ante-mortem and post-mortem factors into the models. These factors can include breed of the animal, production system and environmental elements, use of growth promoters, slaughterhouse conditions as well as post-mortem aging period. This might be the reason why our R-squares for different sensory attributes, especially tenderness is not as high as the authors stated. Having said that, our prediction models captured influential factors with reasonable explanatory power (0.39-0.48 for sensory tenderness at different post-mortem aging days) which can be used for future developments on meat quality prediction models.

Hocquette et al. (2014) stated that shear force is associated with tenderness of the meat. As less tender meat contains more collagen and cross-sectional areas of muscle fibers. While the tenderer the meat, the amount of insoluble collagen would be less, and a considerable mitochondrial enzyme activity could be seen. Other researchers reported that total 2% of sensory panel scored tenderness in *Longissimus thoracis* muscle, that can be explained by levels of total collagen content, metabolic activities of the muscle, levels of muscle fat content as well as muscle fiber areas (Chriki et al., 2013). These statements are in agreement with findings in the present study where WBSF and fat content were significant for sensory tenderness and connective tissue in different post-mortem aging days with model R-squared between 0.39 to 0.48 for tenderness and from 0.18 to 0.34 for connective tissue.

Hocquette et al. (2010) reviewed that muscle fat content is related to flavor and juiciness of the meat products and will increase it, however these relationships between fat content and flavor can be curvilinear. Differences in levels of fat content in highly variable datasets, can be only responsible for 16% of flavor variability (Thompson, 2004) while in low variable datasets this amount would be reduced to 3% (Hocquette et al., 2011). The results from our prediction models showed that fat content is significant for meat flavor intensity and off-flavor in different days of post-mortem aging but the model R-squared obtained was commonly low (ranging from 0.13 to 0.21) which indicates marginal contribution of fat to sensory, juiciness, and flavor.

Gagaoua et al. (2019) in a study on comprehensive modeling for prediction of tenderness, after filtering and excluding unimportant variables, included 24 important elements in their model. They reported that the variability in WBSF was originated from environmental factors (i.e., hay or grass diet, weaning age, and animal type), slaughterhouse circumstances, meat level (pH, color attributes) as well as muscle level proteins (using protein biomarkers related to tenderness). These findings are in agreement with our study where contemporary groups (which classifies animals for different environmental factors from farm to slaughterhouse conditions), sex, and in some cases pH and color indices were significant regarding sensory attributes.

Ferguson et al. (2001) reported that many ante and post-mortem elements are affecting tenderness of the meat. These factors include animal breed, sex, age, rearing conditions as well as post-mortem aging and circumstances. Our findings are in agreement with their research results as most of our fixed effects were significant for predicting sensory attributes.

Researchers studying the effects of ante and post-mortem factors in predicting meat quality reported that elements such as aging period of the meat, animal breed, finishing treatments and interactions between them captured around 50% of variation in sensory tenderness and juiciness (Juárez et al., 2012). The R-squared values that we found for these two sensory traits were 0.39-0.48 for tenderness and 0.20 for juiciness. Considering that we used different elements, these results are partially in agreement with our findings.

There are still potential factors that could be incorporated into prediction models that we developed. These information are namely biochemical information, different post-mortem aging periods as well as muscle profiling, and other biological information such as solubility of connective tissue, types of muscle fibers, and proteolysis. In addition, there might be other objectively measure traits that could be used. If available, these elements could be integrated with our developed model in order to acquire a better predicting model that can be used the beef industry aiming to replace sensory panel measurements with objectively measured traits such as WBSF or fat content.

4.5. Conclusion

Many factors have been reported that can potentially be influential on beef sensory attributes including tenderness and flavor which has been reported to be very important in consumer's satisfaction and determinant of re-purchasing a product. Although, sensory attributes are hard to measure, expensive and labor intensive, they are good measurements of what is consumer's acceptance while objectively measured traits such as WBSF, fat content, and color attributes are relatively easier and faster to perform, studies indicates that they capture one dimensional property of a product and cannot account for all the properties desired for customers. In this study, we investigated the possibility of predicting meat sensory attributes with prediction models that combines all objectively measured traits available as well as fixed effects. The results showed that for almost all sensory attributes WBSF and fat content were significant. On the other hand, color attributes (Chroma and Hue) were not consistently significant for sensory traits. Altogether, considering different factors integrated in our prediction models the obtained R-squares were reasonable and can be used for future studies.

Our approach in this study produced fairly good results and still needs some additional work so it can be implemented into beef industry in order to achieve the goal of predicting sensory attributes without going through sensory measurements and replacing it with objectively measured traits. The mentioned ultimate goal gives industry the ability to process large number of samples at a much lower cost as well as being faster in performing and predicting desired attributes in beef. This can attract the interest of stakeholders in beef industry for producing consistent high quality beef meat that can satisfy consumer demands and benefit the producers at the same time.

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Table 4. 1 Predicting Sensory attributes measured at day 3 post-mortem from objectively measured traits measured at day 3 post-mortem.

	Overall tenderness day3	Overall palatability day3	Connective tissue day3	Sustain juiciness day3	Flavor Intensity day3	Off-flavour day3
Warner-Bratzler shear force, day3	***	***	***	**	***	***
Fat content, day3	***	***	***	***	***	.
Meat pH, day3	ns	ns	ns	ns	ns	***
Chroma saturation index of color, day3	***	***	*	ns	ns	ns
Color of the meat hue angel, day3	ns	ns	**	*	ns	**
Slaughter Age	***	***	ns	***	***	ns
Animal sex	***	ns	***	ns	ns	*
Contemporary Group	***	***	***	***	***	***
Continental Breed Fraction	ns	ns	ns	ns	ns	ns
British Breed Fraction	*	ns	ns	ns	ns	ns
Model R-squared	0.48	0.36	0.34	0.22	0.21	0.17

Significancy codes: ‘***’ 0.001, ‘**’ 0.01, ‘*’ 0.05, ‘.’ 0.1, ‘ns’ not significant

Table 4. 2 Predicting Sensory attributes measured at day 29 post-mortem from objectively measured traits measured at day 29 post-mortem.

	Overall tenderness day29	Overall palatability day29	Connective tissue day29	Sustain juiciness day29	Flavor Intensity day29	Off-flavour day29
Warner-Bratzler shear force, day29	***	***	***	***	***	***
Fat content, day29	ns	***	**	***	***	**
Meat pH, day29	*	**	***	***	ns	.
Chroma saturation index of color, day29	ns	**	ns	*	***	**
Color of the meat hue angel, day29	**	ns	**	ns	ns	ns
Slaughter Age	***	*	ns	***	**	**
Animal sex	***	ns	**	ns	ns	ns
Contemporary Group	***	***	***	***	***	***
Continental Breed Fraction	ns	ns	ns	ns	ns	ns
British Breed Fraction	ns	ns	ns	ns	*	ns
Model R-squared	0.39	0.25	0.18	0.20	0.21	0.13

Significancy codes: ‘***’ 0.001, ‘**’ 0.01, ‘*’ 0.05, ‘.’ 0.1, ‘ns’ not significant

Table 4. 3 Predicting Sensory attributes measured at day 29 post-mortem from objectively measured traits at day 3 post-mortem

	Overall tenderness day29	Overall palatability day29	Connective tissue day29	Sustain juiciness day29	Flavor Intensity day29	Off-flavour day29
Warner-Bratzler shear force, day3	***	***	***	***	***	**
Fat content, day3	**	***	ns	***	***	***
Meat pH, day3	ns	*	ns	ns	*	***
Chroma saturation index of color, day3	***	ns	*	.	*	ns
Color of the meat hue angel, day3	*	ns	***	*	ns	ns
Slaughter Age	***	***	ns	***	***	***
Animal sex	***	ns	**	ns	ns	ns
Contemporary Group	***	***	***	***	***	***
Continental Breed Fraction	ns	ns	ns	ns	ns	ns
British Breed Fraction	ns	ns	ns	ns	*	ns
Model R-squared	0.39	0.23	0.20	0.20	0.21	0.14

Significancy codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1, 'ns' not significant

Chapter 5. Summary and general conclusions

5.1. Summary of results

5.1.1. Overview

Meat palatability attributes are important for consumer satisfaction (Leal-Gutiérrez and Mateescu 2019; Bearden and Teel 1983), but its improvement is challenging because they are controlled by many genes and influenced by environmental effects (Gill et al. 2010; Suman and Joseph 2013). Many factors influence them and due to low to moderate heritability estimates it is harder to perform genetic selection on them (Listrat et al. 2016; Leal-Gutiérrez and Mateescu 2019; Gredell et al. 2018; Sitz et al. 2005). In this study we investigated the sensory (overall tenderness and palatability, connective tissue, flavor intensity and off-flavor as well as juiciness) and objectively measured traits (WBSF, fat content, color and pH) of Canadian commercial crossbred beef cattle, after 3 and 29 days of post-mortem aging. Pearson correlation coefficient, variance components and genetic parameters including heritability and genetic correlations were estimated for these traits. Lastly, with putting together all the objectively measured traits in a prediction model we estimated how much variation can be captured from these traits and fixed effects (comprising environmental effects) to predict the changes in sensory attributes.

5.1.2. Significant findings and general conclusion

Different studies indicated that aging of the meat for 28 days will result in more tender and palatable meat. On the other hand, the differences in meat palatability attributes improvement after 35 days of aging does not greatly differ from 28 days of aging, and it will not offset the cost of the extended aging for industry as the price will probably still stay the same as 28 days aged product. In addition, aging for more than 35 days will increase the chance of developing off-flavor properties due to lipid oxidation and hence lower consumer acceptability and even rancidity detection in longer extended post-mortem aging periods (up to 20 weeks) (Kline 2015; Garmyn et al. 2020; Picard and Gagaoua 2017; Warriss 2000). For these mentioned reasons we chose 29 days of post-mortem aging to achieve the optimum quality without enforcing extra cost into the meat industry.

Pearson correlation coefficients indicated that overall tenderness and fat content as well as WBSF and lightness and Hue of the meat had moderate to strong correlations (respectively) between day 3 and 29 of their measurements. These results indicate that between all sensory and objective measured traits, overall tenderness, fat content, WBSF, lightness and Hue are consistent over post-mortem aging period. Thus, early assessments for these traits could be used as good indicator of their changes after 29 days of aging. These early assessments are important for better understanding of changes in meat palatability attributes in early stages of post-mortem aging, and in combination with extended aging period data (i.e., 29 days), we might be able to predict changes in palatability attributes. Other phenotypic correlations between palatability traits were weak which points at their inconsistency and change during the aging period and early measurements day 3 post-mortem are not a good indication of changes in palatability traits later on at day 29 post-mortem and hence the final quality of the beef. This inconsistency in beef products is important as it has been reported to be the number one quality concern in national beef quality audit in Canada for consumers (Beef Cattle Research Council 2018).

These results also indicate that with only considering the phenotype of the traits and ignoring relationship between animals, these palatability attributes seem to not be associated together. For a better understanding of relationship, we looked further into genetic parameters estimations and associations between meat quality traits, both objective and subjectively measured attributes.

With genetic associations between these traits, we could understand that they might have common genes and pathways controlling them which is useful for genetic selection for next generations in order to improve these traits.

The results from genetic parameter estimation from this thesis suggested that overall tenderness (day 3 and 29 post-mortem) and overall palatability (day 3 post-mortem) were moderately heritable in Canadian commercial crossbred cattle. Among the 12 objective measured traits fat content, WBSF, lightness and Hue were highly heritable at both day 3 and 29 post-mortem.

Analysis of color attributes for day 0, 2 and 4 of display life showed that lightness, Hue and Chroma had negligible heritability estimates. Low heritability estimates for these traits indicates that color indices in different shelf life days are mainly affected by environmental factors. Looking at their trend over 3 different display days on retail shelf life, colour was observed to drastically decline after day 2 (P-value<0.001) which indicates unfavorable beef color changes after day 2 of display. This means overall, the best day of the display for beef products in the market is up to 2 days and after that the color quality attributes start to deteriorate.

For a more in depth understanding of associations between traits in order to improve beef quality through selective breeding programs and finding possible levels of pleiotropic gene effects controlling distinct traits simultaneously, genetic correlations were estimated. One major hypothesis that we tested in this thesis was whether sensory attributes are genetically associated with objective measured traits, hence we look into genetic correlations of sensory assessed traits with different objective measured traits. Genetic correlation estimation between our subjective and objective traits suggested that WBSF at day 3 post-mortem had strong (>0.6) negative genetic correlation to overall tenderness, overall palatability, and connective tissue at day 3 post-mortem as well as overall tenderness day 29 post-mortem. Also, WBSF at day 29 post-mortem had negative and strong (>0.6) correlations to overall tenderness and connective tissue at day 29 post-mortem. The more the meat is tender, with less connective tissue, the less is the force used for shearing through the meat and hence higher palatability in the product.

In addition, strong positive genetic correlations between fat content (days 3 and 29 post-mortem) with flavor intensity and off-flavor (at both days 3 and 29 post-mortem) and overall palatability (at day 29 post-mortem) were found. Additionally, our results suggested that at day 3 post-mortem moderate genetic correlations between lightness with connective tissue, Chroma with overall tenderness and connective tissue existed. At day 29 post-mortem Chroma was moderately correlated to off-flavor and overall palatability. The fact that sensory flavor and off-flavor attributes are associated with fat content can be explained by fat soluble compounds present in beef. Which over time, may develop off-flavor due to oxidation of the fat substance. Lastly, the relationship between lightness and Chroma (color saturation index) with connective tissue and overall tenderness indicates that the more the meat is tender, myofilaments are less compact in their place, and the less connective tissue present, there is more levels of light reflected by the surface of the meat, and hence it appears more appealing.

From these results we can conclude that WBSF is related to overall sensory tenderness, palatability and connective tissue. This means that these traits have common genes and pathways and are affecting each other, thus in breeding programs these effects should be considered. This information can be useful for finding synergy and antagonism relationship between traits of interest and optimize genetic selection for the best results possible to achieve improvement in all beef quality aspects. More importantly, these results were obtained from large sample of Canadian commercial crossbred cattle which can be useful for having a better understanding of the relationship between these traits on the very end product of selection in pure breed cattle in Canada.

Our results for prediction analysis indicated that WBSF and fat content were both mostly significant for sensory attributes. Among the fixed effects, slaughter age showed to be commonly significant. Meat pH and color attributes were not consistently significant in prediction models during post-mortem aging. The R-squared values obtained from our prediction study indicated that the factors used in our models captured 36-48% of variation in overall tenderness and palatability. This indicates that these objectively measured traits (WBSF, fat content, in some cases color Chroma and Hue attributes) could be good potential approaches for developing prediction tools for sensory attributes. Thus, we can use this information to predict sensory attributes in different days of post-mortem aging (3 and 29) from objectively measured traits. This is especially helpful as sensory attributes are very important in meat industry for consumer satisfaction and their choice for purchasing and re-purchasing of a product while their measurements are costly, labor intensive and time consuming. On the other hand, the objectively measured attributes are relatively easier to take place, non-invasive, less time consuming and generates a large amount of data in short period of time.

One of the strengths of our work was its focus on composite commercial cattle breeds compared to previous works done on pure bred animals. This is important because the composite breed animals are usually used to have advantage of crossbreeds. These advantages are having a diverse gene pool, which is helpful for selection of the best animals for improving meat quality traits, and the ability to work on different traits simultaneously to be improved for example, working on meat palatability and feed efficiency at the same time. Our work showed the strength and direction of relationships between objective and subjective traits in composite breed population of beef in Alberta. This study showed the changes in palatability attributes in commercial crossbreeds which are the end product of implemented genetic selection on pure breeds. Thus, the challenges of breed part in their selection can be handled as different breeds are used for producing crossbreeds and our results also can be used for better genetic selection on pure breeds in future breeding programs for meat quality improvement in beef.

Based on these findings we can conclude that objectively measured traits such as WBSF, fat content, and color measurements can potentially be useful for predicting meat sensory attributes including tenderness, palatability and flavor attributes at day 3 and 29 post-mortem.

These results collectively showed that there are levels of pleiotropy between these traits and many genes are influencing these complex traits. Based on genetic correlation estimates it is possible to have genes with additive effect affecting distinct traits simultaneously and this information can be used in breeding programs. In addition, these studied traits have moderate to high heritability estimates which means they are good candidates to be incorporated into breeding programs for enhancing meat quality attributes in multibreed beef cattle.

5.2. Future work and study limitations

In this thesis strong genetic associations of sensory tenderness, palatability and connective tissue with WBSF were found, in addition genetic correlations were shown for fat content to flavor and off flavor, and color measurements to connective tissue, tenderness and palatability. In all studies, a total of 1,200 multibreed animals were used and as it has been mentioned before, breed composition has a tremendous effect on meat quality and palatability attributes. Considering this fact, a suggestion for future studies could be using other crossbreed populations, with a larger sample size for estimating beef quality attributes as well as increasing the number of animals with sensory traits to improve the prediction analysis. This information can be used in combination with our results, as well as detailed information of ante and post-mortem circumstances for developing prediction models. To achieve a better prediction model in this regard, larger sample size and including variables into the model would be useful. These variables could be from ante-mortem conditions such as management, diet, level of stress to slaughter, animal handling information, slaughter conditions and post-mortem such as storage, temperature, humidity, aging duration and conditions, and velocity to other detailed information of biochemical profiling of the meat. With including more information, more variation would be captured in prediction models and so a better R-squared could be obtained and, at the end a generalized prediction model for sensory attributes could be available to the meat industry.

To improve our knowledge regarding the genetic and genomic background of the studied traits, the genomic relationship matrix based on SNP markers could be incorporated for variance component analysis, heritability and genetic correlation estimations. The prediction models in our study expand our knowledge about sensory attributes and their relation to objectively measured traits which opens new doors for animal breeding regarding meat quality attributes. All the information obtained in this thesis, in combination with economic data can be used to develop selection index equation including some key quality traits and consistency of beef meat, allowing to incorporate it into Canadian crossbred genetic selection programs. Next steps for this study could be to look into genome and protein biomarkers. Detecting genes that are affecting palatability attributes using genome-wide association studies (GWAS). In addition, identifying genes with pleiotropic effects not only on palatability attributes but also with traits that are already being measured such as feed efficiency to speed up the genetic improvement in several traits simultaneously. Further, implementing genomic selection to predict the phenotype of young animals or those that will be used as parents of the next generation (so they will not be slaughtered), and end with a multi-trait selection index that combines several traits to improve meat quality attributes. The relationship between sensory traits and regular production traits can be used in selection index such as average daily gain (ADG), backfat and etc. can be investigated in future studies. Genetic and phenotypic relationship between traits have direct effect on the optimized selection for maximum profit for producers using selection index. For example, there is an unfavorable antagonistic relationship between backfat and marbling score. This information can be used to optimize selection for antagonistic traits as well.

The determination of genetic merit of animals with DNA sample upon birth using genomic prediction technique can help in pre-selection of animals. It would help to have faster genetic gain in economic traits. Thus, comprehensive additional research should take place to provide an in-depth knowledge for genetic selection which can provide a consistent good quality product for consumers These works still remains to take place in time, but undoubtedly our findings can contribute to development of tools to improve meat quality in beef and their applications afterwards and to address the lack of consistency and concerns about meat quality reported in National Beef Strategy.

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