BOARD INVITED REVIEW

Biology, strategies, and fresh meat consequences of manipulating the fatty acid composition of meat

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Abstract

The utility and attractiveness of adipose tissue within meat products vary based on species, cut, and consumer preference. In beef, producers are rewarded for producing carcasses with greater visual marbling at the 12th and 13th rib juncture, while pork producers are either not rewarded or penalized for producing carcasses with too much adipose tissue. Some consumers prefer to purchase leaner meat cuts, while other consumers pay premiums to consume products with elevated fat content. While no clear consumer adipose tissue preference standard exists, advances in beef and swine nutrition have enabled producers to target markets that enable them to maximize profits. One niche market that has increased in popularity over the last decade is manipulating the fatty acid profile, specifically increasing omega-3 fatty acid content, of beef and pork products to increase their appeal in a healthy diet. While much research has documented the ability of preharvest diet to alter the fatty acid profile of beef and pork, the same studies have indicated both the color and palatability of these products were negatively affected if preharvest diets were not managed properly. The following review discusses the biology of adipose tissue and lipid accumulation, altering the omega-3 fatty acid profile of beef and pork, negative fresh meat color and palatability associated with these studies, and strategies to mitigate the negative effects of increased omega-3 fatty acid content.

Key words: adipose, beef, color, fatty acid, palatability, pork

Introduction

Visceral and subcutaneous fat depots are largely removed during harvest and processing, thereby making their contribution to dietary fat consumption minimal. The intramuscular and intermuscular fat depots are the primary depots that contribute to fat in intact whole muscle meat products consumers purchase. Within the muscle, dietary lipids can be attributed to the lipids stored in intramuscular adipocytes (marbling), which lie within the perimysial connective tissue layer closely associated with muscle fiber bundles, as well as intramyocellular lipids, which

lie within individual muscle fibers. Together these two sources make up the bulk of the extractable lipid present within a given skeletal muscle. Depending on where fat lies on the carcass and species, fat can add or remove value from the carcass and fresh meat products.

Sans and Combris (2015) demonstrated that world per capita consumption of meat rose from 61 to 81 g over a 50-yr period ending in 2011. The authors identified economic progress as one of the major catalysts of this increase in consumption. In consumer research conducted at Kansas State University,

Abbreviations

ALA	alpha-linolenic acid
DHA	docosahexaenoic acid
EPA	eicosapentaenoic acid
LL	longissimus lumborum
LT	longissimus thoracis
MUFA	monounsaturated fatty acids
PUFA	polyunsaturated fatty acids
SFA	saturated fatty acids
TBARS	Thiobarbituric acid reactive substances

participating consumers are commonly asked about their purchasing motivators. These research studies indicated midwestern consumers placed the importance of the nutritive value of meat from 52 to 55 on a 100-point scale with 100 designated as being extremely important (Wilfong et al., 2016a, 2016b; Vierck et al., 2018; Olson et al., 2019; Prill et al., 2019). In Europe, Wezemaal et al. (2014) reported consumers valued meat nutritional claims based on country. Tonsor et al. (2010) identified information linking meat and human health (fat, cholesterol, heart disease, etc.) had significant impacts on meat demand. While Curan (2013) reported consumers were willing to pay more for a familiar product such as grass-fed beef, they were willing to pay a US \$0.84 and US \$0.35/kg premium for omega-3 enhanced steaks and ground beef, respectively. More importantly, the author found consumers were willing to pay more for omega-3 products, the more they were educated about the associated health benefits of omega-3 fatty acids. Therefore, altering the nutritive value of meat has become the focus of producers who hope to capitalize on the premiums associated with these niche markets.

Biology of altering the fatty acid profile of meat

The cellularity of adipose tissue and the adipocyte

Adipose tissue, a heterogeneous tissue consisting of cells from the adipocyte lineage, exists on a continuum of maturation ranging from immature adipo-fibroblast precursors to mature adipocytes filled with lipid (Vierck et al., 1996; Fernyhough et al., 2008; Hausman et al., 2009). Preadipocytes contain multilocular lipid droplets that have not yet coalesced to form a single lipid droplet. Mature adipocytes consist of a centrally located, unilocular lipid droplet composed of lipid from both endogenous and exogenous sources. The size of adipocytes varies with physiological status, genetics, and age; however, adipocytes generally demonstrate a biphasic (small and large) distribution in livestock and other species (Allen, 1976; Etherton, 1980; Björnheden et al., 2004; Jo et al., 2009). The size of the lipid droplet can range from 0.1 to over 200 μm^2 in eukaryotes (Schott et al., 2019). The assimilation of lipids into the large lipid droplet results in peripheral displacement of the nucleus in the mature adipocyte, which speaks to the importance of storage capacity to the functionality of this specialized cell type. Other organelles, including the endoplasmic reticulum, mitochondria, and Golgi apparatus, are present to allow for the synthesis of endogenous lipids, production and secretion of adipokines, as well as oxidative nutrient metabolism (Cushman, 1970). In addition to the present adipocyte population, adipose tissue also possesses a substantial amount of innervation and blood vessels (Hausman and Richardson, 2004), macrophages (Shoelson et al., 2007; Gericke et al., 2015), and other cell types. This cellular milieu results in an active and dynamic metabolic environment (reviewed by Scherer, 2006) which must be capable of accepting,

storing, synthesizing, and releasing lipid on demand depending on the metabolic and physiological status of the animal (Church et al., 2011; Wang et al., 2017).

Adipose tissue is a relatively amorphous tissue that is compartmentalized in discrete depots throughout the body. These include the visceral, subcutaneous, intermuscular, and intramuscular depots found closely associated with other organs and tissues. These depots are metabolically distinct with each one exhibiting different intrinsic metabolic and biochemical paradigms based on their location and functionality (Smith and Crouse, 1984; Smith et al., 1998). These molecular peculiarities make depots independently amenable to environmental and nutritional cues (Smith and Crouse, 1984); however, the specific mediators of these metabolic programs remain elusive (Hausman et al., 2009). This is the driving force behind contemporary adipose tissue research because an ability to manipulate individual depots independently of others would have substantial biomedical implications and would drastically improve production efficiency and carcass quality. While there are certainly biological implications to the amount and composition of various adipose depots and their constituent lipids, there are also meat quality and consumer ramifications that are impacted by fatty acid composition. The lipids that make up the stored lipid in these depots include those from both exogenous and endogenous origins.

Exogenous lipids

Exogenous lipids arise from dietary sources and are digested, metabolized, and incorporated into lipid reserves. Diets fed to livestock utilize fat sources ranging from beef tallow to sunflower oil (Kerr et al. 2015; Paulk et al., 2015; Kellner and Patience, 2017). The choice of the fat source is often one of economic and regional availability, which can impact the consistency of products produced nationally and internationally (Kellner et al., 2017). These fat sources have a range of fatty acid content and composition, and as such have a differential impact on the overall quantity and composition of lipids deposited in meat animal carcass tissues (Mello et al., 2012; Kellner and Patience, 2017). Dietary lipid digestion and absorption are dependent on species-specific digestive anatomy and physiology (Nafikov and Beitz, 2007), which dictate the efficacy of management and nutritional strategies on changing carcass composition.

Dietary lipids that are digested and metabolized in nonruminant animals are largely represented in the meat from pork carcasses (Stephenson et al., 2016; Kellner and Patience, 2017). Fats are added to swine diets for a variety of reasons and the benefits include decreased feed intake, increased ADG, and improved feed efficiency (De la Lata et al., 2001). In monogastrics such as swine, the source (Apple et al., 2009) duration of feeding (Xu et al., 2010) and withdrawal period from fat sources (Browne et al., 2013; Stephenson et al., 2016) affected the lipids deposited and ultimately represented in the pork carcass. This has implications at the processor level in which highly unsaturated pork products are less desirable (Benz et al., 2010) because of their impact on shelf-life due to increased potential for oxidative rancidity. Additionally, numerous studies demonstrated dietary fat sources which increased fat unsaturation, negatively impacted belly, the most economically important wholesale primal, firmness (Rentfrow et al., 2003; Teye et al., 2006; Apple et al., 2007). Belly firmness is important to the industry, as it impacts yield and product quality and consistency. Soybean oil, for example, is a highly unsaturated fat source often included in swine diets depending on the cost and availability. Feeding

soybean oil for extended durations during the grow-finisher phases can negatively impact the fatty acid composition of the belly, jowl, and backfat depots (Stephenson et al., 2016).

Swine diets are formulated in phases to maximize the metabolic and minimize the economic impact of the ration. Producers routinely source ingredients based on these principles and as such consider feeding and withdrawal strategies to reconcile the cost of gain with composition of gain during the grower and finisher phases of production. Based on depot-specific metabolism, these strategies are more effective in some depots compared with others because not all depots are equally modified by dietary lipid and some appear refractory to lipid turnover. Feeding soybean meal followed by a withdrawal period caused an increase in iodine value, which is a measure of fatty acid desaturation in pork cuts, compared with a diet with beef tallow as the fat source, which is more saturated in composition. Still, there was a reduction in iodine value when soybean oil was withdrawn in the latter portion of the finishing phase indicating some turnover of exogenous lipids deposited in the backfat, jowl, and belly fat depots (Figure 1; Stephenson et al., 2016).

Because of their monogastric physiology and direct incorporation of dietary lipids into tissues, swine nutritionists have developed numerous regression equations to predict the fatty acid composition of carcass tissues based on the composition of the diet (Paulk et al., 2015; Kellner et al., 2017). With sufficient information regarding the feed composition and physiological status of the animal, these equations can predict carcass fat composition with relative accuracy and have become a valuable tool in meeting industry demands (Benz et al., 2010).

Ruminants pose a more complex challenge when it comes to predicting carcass composition based on feed ingredients

and the composition of dietary lipids. Ruminant diets typically contain low fat (less than 5%) because of the negative impact on rumen fermentation. This poses one limitation on the contribution of dietary fat to tissue composition. Ruminants are fed diets consisting of forages and cereal grains and whether they are forage or concentrate based, polyunsaturated fatty acids (PUFA) are the predominant fatty acids present (Dewhurst et al., 2003; Lourenço et al., 2008). The second limitation on deposition of dietary fats in ruminant tissues is rumen microbes have the first opportunity to metabolize these lipids before they are available for deposition. As a result, despite the PUFA content of the diet, the triacylglycerol composition of beef contains much more saturated fatty acids (SFA) and monounsaturated fatty acids (MUFA) than PUFA due to microbial intermediary metabolism of dietary fatty acids followed by intermediary metabolism by the animal itself. PUFA are toxic to rumen microbes (Maia et al., 2010) and as a result, they are rapidly hydrogenated to render them less detrimental to the rumen microbial environment (Harfoot and Hazlewood, 1988). The result of this microbial metabolism is an increased proportion of lipid substrates different from those in the diet that are available to be metabolized by the animal. Still, precision management strategies and novel feed ingredients (Phelps et al., 2016a) that can resist the metabolic intervention by rumen microbes can increase the deposition of dietary lipids in carcass tissues or alter them in a more predictable manner. In addition to forages, distillers grains have increased in prevalence in beef diets due to their availability, economic value, and nutrient density. Approximately, 42% of distillers grains used in livestock feed are used in beef production. The PUFA content in distillers grains is partially protected from rumen biohydrogenation (Vander Pol et al., 2009) and feeding distillers increases the PUFA content of beef (Mello et al., 2012).

Figure 1. Effect of dietary fat source and withdrawal period on pork jowl, belly, and backfat iodine value. Finishing pigs ($N = 160$; PIC 337 $\times$ 1050; initial BW of 45.6 kg) were used in an 84-d finishing trial with two pigs per pen and eight pens per treatment. Diets were fed in two phases with phase 1 fed days 0 to 42 and phase 2 fed days 42 to 84. Control, corn–soybean meal diet with no fat; Tallow, 4% beef tallow; Soy, 4% soybean oil. Iodine value = $[C16:1] \times 0.9502 + [C18:1] \times 0.8598 + [C18:2] \times 1.7315 + [C18:3] \times 2.6125 + [C20:1] \times 0.7852 + [C22:1n-9] \times 3.2008 + [C22:5n-3] \times 3.6974 + [C22:6n-3] \times 4.4632$; brackets indicate concentrations. There was a significant feeding period (days 0 to 42 vs. days 42 to 84) $\times$ fat source (tallow vs. soybean oil) interaction ($P < 0.01$). Adapted from Stephenson et al. (2016).

Endogenous lipids

Endogenous lipids are those synthesized *de novo* using carbons from carbohydrates, amino acids, acetate, and other metabolite precursors. Dietary amino acids and carbohydrates in excess of metabolic needs can be converted to fatty acids for storage in neutral lipids and be released upon metabolic demand for the animal. When monogastric diets are not balanced appropriately for ratios of protein:energy or for adequate amounts of essential amino acids, an increased amount of dietary protein (amino acids) and/or carbohydrates can be diverted to storage in the form of fatty acids through *de novo* lipogenesis. In ruminants, in which dietary fat content is relatively low, endogenous synthesis of long-chain fatty acids from volatile fatty acids (less than six carbons), namely acetate, is also a major contributor to endogenous lipid synthesis (Bergen and Mersmann, 2005).

In addition to *de novo* synthesis, lipids synthesized as a result of modifying dietary lipids through elongation, desaturation, or oxidation also contribute to the endogenous lipid fraction. These lipids are deposited in adipose tissue and are incorporated into triglycerides along with exogenous dietary lipids to yield the full complement of lipids present in carcass tissues. The extent to which endogenous lipids contribute to lipid filling and adiposity are dependent on diet composition, nutrient (protein and energy) balance, and physiological status of the animal.

Enzymes such as desaturases and elongases are important in ruminants which absorb high amounts of oleic and palmitic acids as a result of microbial biohydrogenation of PUFA in the rumen (Chung et al., 2006). The SCD enzyme converts substrates such as stearic acid (an 18 carbon SFA) into oleic acid (an 18 carbon MUFA) through desaturation at the Δ^9 position to generate MUFAs which are present at a relatively high amount in ruminant tissues (Chung et al., 2006; Dinh et al., 2010). For example, the composition of beef marbling has 43% SFA, 50% MUFA, and 7% PUFA, with oleic acid making up nearly 40% of the total MUFA present (USDA, 2018). These data indicate the importance of endogenous metabolism to the total lipids present in carcasses.

Lipid storage and release from adipose tissue

Regardless of their endogenous or exogenous origin, the fats present in meat products are the result of lipid molecules deposited in carcass tissues. These lipids are essential cellular components and through the combination of dietary provision, endogenous synthesis, lipid recycling, and salvage pathways provide the necessary energy repositories and signaling molecules involved in normal metabolism. They occur in various forms due to the interaction of normal physiology, nutrition, and positive energy balance. Whether they come from endogenous or exogenous sources, the bulk of the lipids that make up adipose depots and other lipid repositories are stored in subcellular lipid droplets. These bona fide organelles are metabolically active and consist of a nonpolar lipid core and a polar phospholipid bilayer (Kuverschner et al., 2008). These droplets accept, store, and release lipids on-demand in response to the metabolic disposition of the animal (Kuverschner et al., 2008). The lipid droplet is, therefore, a dynamic organelle that lies at the nexus of catabolism, storage, and biosynthetic metabolism of lipid-derived metabolites, hormones, and signaling molecules (reviewed in Guo et al., 2009; Walther et al., 2012).

The lipids in these droplets can be further classified based on their chemical properties including their degree of saturation and chain length in the case of individual fatty acids, and their polarity in the case of triacylglycerides (triglycerides)

and phospholipids. Free fatty acids are hydrocarbon chains characterized by a methyl end and a carboxylic acid end that can be reactive and even cytotoxic in the intra- and extracellular milieu (Savary et al., 2012). To neutralize this reactivity, and limit cytotoxicity of free fatty acids, they are stored as triacylglycerides (triglycerides) and cholesteryl esters within the lipid droplet (Listenberger et al., 2003). Triglycerides make up the largest portion of lipids present in the droplet. These neutral lipids are synthesized through either the glycerol phosphate pathway or the monoacylglycerol pathway to esterify free fatty acids from endogenous and exogenous origins with a glycerol moiety derived through glycolysis or other metabolic pathways (Takeuchi and Reue, 2009).

The glycerol moiety can also be modified to generate phospholipids through the substitution of hydrogen on the *sn*-1 methyl carbon with a phosphate group to create an amphiphilic molecule that functions in membrane synthesis and stabilization. Because of their amphiphilic structure, these phospholipids can be separated from total lipids through chemicals and are present in the polar lipid portion upon fractionation. In contrast to lipids isolated from subcutaneous fat, marbling contains relatively more phospholipids, perhaps due to their association with proteins as lipoproteins or proteolipids in this tissue (Rhee, 2000; Aberle et al., 2003). Phospholipids serve a structural role in helping to form the cellular membranes and that of the intracellular lipid droplet. As such, they contribute to the overall lipid composition of meat products as adipocytes and ectopic lipid droplets expand. Still, the relative contribution and dynamics of this fraction in meat products remain relatively small compared with that of the neutral fraction as the droplet enlarges as a result of neutral lipid deposition in the cell (Warren et al., 2008).

Quality grade is based largely on the amount of intramuscular fat present in the loin muscle. The amount of fat in intramuscular fat increases resulting in visible flecks used to assign marbling scores. In other words, quality grade improves as the amount of lipid in the lipid droplet of intramuscular adipocytes increases. In addition to these changes in lipid volume, there are demonstrable changes in fatty acid composition as intramuscular fat (quality grade) improves in beef carcass (Legako et al., 2015a). When lipids were extracted from raw strip steaks from USDA Prime, low Choice, or Standard quality carcasses, there was an increase in deposition in the neutral lipid fraction compared with the polar fraction which remained relatively constant regardless of quality grade (Legako et al., 2015b). Warren et al. (2008) reported that in samples containing a range of 41 to 96 mg of total lipid per gram of sample, there was a relatively constant concentration of 7 mg of phospholipids per gram of wet sample. These data are consistent with that of Wood et al. (2008) who reported similar profiles across degrees of intramuscular fat. In terms of composition, neutral lipids are enriched in SFA and MUFA compared with the polar lipid fraction which has higher PUFA concentrations (Itoh et al., 1999; Scollan et al., 2006). Regardless of fraction, as total fatty acid increases, the PUFA concentration decreases while the SFA and MUFA content increases (Wood et al., 2008).

Altering the fatty acid profile of red meat products (omega-3 fatty acids)

In the United States, meat contributes more than 40% of daily protein intake and 20% of daily fat intake. The fatty acid profile of meat products is primarily MUFAs and SFAs and very low amounts of PUFA; however, the 2015 Dietary Guidelines for

Americans suggests less than 10% of calories should originate from SFA and encourages consuming at least 250 mg of omega-3 PUFAs daily. The most common omega-3 FA recommended for consumption include alpha-linolenic acid (ALA) which is found in flaxseed and eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) which are found in seafood products. Unfortunately, most Americans are not consuming adequate amounts of these FA.

Because of this, some researchers have focused on manipulating FA profiles of red meat to achieve greater amounts of omega-3 FA. The main strategies used to manipulate the fatty acid profile of meat is through the dietary supplementation of oilseeds, plant oils, fish oil, marine algae, and fat supplements. Although beneficial from a health standpoint, PUFA are more susceptible to oxidation and oxidation of these FA can lead to myoglobin oxidation during shelf-life causing surface discoloration. This is an issue as meat color is most often used as an indicator of product freshness and quality when consumers purchase at the retail case. The following sections highlight the ability of different supplementation strategies to increase the amount of omega-3 PUFA in red meat products, the potential color issues that arise when omega-3 PUFA are increased, and ways to mitigate these issues.

Flaxseed can be fed both to grazing cattle and finishing cattle as a means to increase ALA levels within beef cuts. Kronberg et al. (2011) reported a 62% and 95% increase in the amount of ALA in longissimus lumborum (LL) steaks when supplementing 10% flaxseed to grazing steers when compared with a conventional grazing diet and corn-soybean meal-supplemented steers, respectively. In a high-forage finishing scenario, Mapiye et al. (2013) reported ALA was increased by 180% within the LL when 14% flaxseed was supplemented to steers on grass hay and red clover diets. When a 10% ground flaxseed was added to a steam-flaked corn feedlot ration, LaBrune et al. (2008) reported a 1.5% increase in ALA within LL steaks when compared with steaks from heifers fed a conventional diet and a diet containing 4% tallow. Maddock et al. (2006) reported feeding 8% flaxseed to heifers in the growing and feedlot phases increased ALA within LL steaks by 197% when compared with steaks from heifers fed diets not containing flaxseed. Similarly, Juárez et al. (2011) reported a 321% increase in ALA within the longissimus thoracis (LT) when steers were fed 10% ground flaxseed.

When fed to pigs, flaxseed products increase ALA levels in the muscle to a greater magnitude. Romans et al. (1995a, 1995b) conducted two studies that demonstrated including up to 15% flaxseed in the diet of finishing pigs increased ALA concentration of the longissimus muscle by up to 358%. Kouba et al. (2003) reported whole-crushed linseed dietary inclusion increased ALA concentration by over 200%. When supplementing oil, Haak et al. (2008) found ALA concentration increased by 125%. This modest increase most likely occurred due to the processing of the oil from the seed.

The beef industry has primarily examined fish oil and fish meal as feed sources to increase omega-3 PUFA. Vatansever et al. (2000) examined the impact of feeding fish oil to feedlot steers on EPA and DHA content of ground beef in both the neutral lipid fraction and phospholipid fraction. The researchers reported that feeding 10% fish oil increased EPA by 43% and DHA by 171% in the neutral lipid fraction. Additionally, Vatansever et al. (2000) reported EPA to be increased by 97% and DHA 75% in the phospholipid fraction. Additionally, Wistuba et al. (2007) reported adding 4% fish oil to feedlot diets increased EPA and DHA in the LL from 0% to 0.08% and 0.06%, respectively. Mandell et al. (1997) reported feeding fish meal to feedlot steers dramatically

(100% to 600%) increased EPA and DHA fatty acids within the LL depending on the amount of fish meal fed (5% or 10%) and the duration it was fed (56 to 168 d). Feeding 5% fish meal for 56, 112, or 168 d resulted in 16, 26, and 29 mg of EPA and DHA/100 g fresh LL, respectively where control levels were 7 mg EPA and DHA/100 g fresh LL. When feedlot steers were fed 10% fish meal, these levels increase to 24, 36.5, and 40.7 EPA and DHA/100 g of fresh LL for 56, 112, and 168 d, respectively.

Givens et al. (2000) reported fish oil/meal to increase DHA and EPA content in beef the most efficiently, but maintaining a consistent, quality source is difficult. There are few studies that have examined the impact of feeding microalgae meal on beef fatty acid profiles. By feeding a microalgae meal from *Schizochytrium limacinum* CCAP 4087/2 to feedlot cattle, Phelps et al. (2016a) reported a 340% increase in EPA levels and 850% increase in DHA levels within the LL when 150 g/d of microalgae meal was supplemented vs. 0 g/d of microalgae meal. In the same study, Phelps et al. (2016b) reported 85/15 ground beef made from knuckles and fat trim from the loin from heifers fed 150 g/d microalgae meal had a 300% and 416% increase in EPA and DHA, respectively when compared with ground beef made from control heifers.

When fed to pigs, aquatically derived feed additives show large increases in DHA and EPA content. Valaja et al. (1992) demonstrated increasing dietary fish meal concentration and duration increased combined DHA and EPA levels by up to 530%. Pigs supplemented with up to 20% tuna fish meal for 28 d had a 165% in all omega-3 FA present in the loin (Howe et al., 2002). Feeding 9 g/kg low-fat fish meal increased EPA and DHA content of the muscle by 55% and 79%, respectively, compared with pigs fed 3 g/kg (Jonsdottir et al., 2003). Haak et al. (2008) reported supplementing fish oil increased EPA and DHA by 523% and 629%, respectively. These divergent responses in DHA and EPA content indicate the fat level and source affect the composition of the meat.

Effects of altering fatty acid profile on fresh meat color stability

Outside of price, color is the single most important attribute consumers use to make purchasing decisions because they utilize it as an indicator of freshness (Mancini and Hunt, 2005). As products are displayed for longer periods, oxymyoglobin (bright-red color) decreases and metmyoglobin increases (brown/gray color). Faustman et al. (1998) stated beef consumers preferred bright, cherry-red color steaks; therefore, maintaining redness during retail display for as long as possible is critical to industry profitability and sustainability. Smith et al. (2000) reported markdowns due to color issues resulted in revenue losses of \$1 billion for the entire meat industry. Adjusting for inflation, in 2019, this number would equate to \$1.5 billion in lost revenue. Fatty acids containing double or triple covalent bonds in their chains are more susceptible to oxidation (Jacobsen, 2008). Oxidation of ALA or EPA and DHA can cause oxidation of the myoglobin pigment leading to the formation of metmyoglobin on the surface of beef products (Jacobsen, 2008). When measured objectively, this leads to meat products having reduced a^* values, increased calculated surface myoglobin percentage, increased hue angle (arctangent of b^*/a^*), or color saturation.

Vatansever et al. (2000) reported ground beef from steers fed linseed, linseed/fish oil, or fish oil had decreased color saturation (increased metmyoglobin) compared with control ground beef, with ground beef from fish oil-fed steers being decreased the most compared with the control. Although a^* values were

similar at the beginning through day 3 of display, LaBrune et al. (2008) reported LL at days 5 and 7 of display, steaks from heifers fed 10% flaxseed had reduced a^* values and increased hue angle compared with steaks from heifers fed control diets. Kronberg et al. (2011) reported no difference in a^* value or hue angle of steaks from steers supplemented flaxseed while grazing, thus indicating supplementation does not work in a grazing system. Phelps et al. (2016a) reported as the level of microalgae was increased in the diet, a^* values decreased linearly from days 2 to 4 of display and quadratically from days 5 to 7. On day 7, LL steaks from heifers fed 100 and 150 g of microalgae daily had a^* values that were reduced by 6 and 10 points, respectively, compared with steaks from heifers fed no microalgae. Using calculated surface metmyoglobin, Phelps et al. (2016a) reported a linear increase in metmyoglobin as the amount of microalgae meal increased from days 0 to 4 of display and this became quadratic from days 5 to 7 of display (Figure 2a). Surface metmyoglobin for steaks in the 100 and 150 g of microalgae fed per day was 42%

and 51% on day 7, respectively whereas the control steaks had 29% surface metmyoglobin on day 7. Similarly, in the ground beef portion of the same study, Phelps et al. (2016b) reported that a^* values of patties made from knuckles and loin fat trim from heifers fed higher amounts of microalgae meal to be reduced from hour 0 to 84 of display, but at 96 h there was no difference in a^* value.

In pork, the effects of altering FA profile on color and color stability have not been as extensively evaluated as they have been in beef. Juárez et al. (2010) reported flaxseed decreased L^* values, possibly through a pH reduction mechanism. In agreement, Jiang et al. (2017) found that linseed oil reduced both L^* and a^* through day 4 of refrigerated storage. Other studies, in contrast, indicated meat color was not affected by dietary linseed inclusion (Kouba et al., 2003; Haak et al., 2008). These data may indicate vast differences in fiber type distribution between pork and beef may be the reason altering the FA profile of pork may not greatly and consistently affect color. Numerous

Figure 2. Effect of dietary microalgae meal on beef longissimus lumborum steak surface metmyoglobin accumulation. (a) Data adapted from Phelps et al. (2016). Finishing heifers were supplemented with 0, 50, 100, and 150 g/heifer $\cdot$ day $^{-1}$ of microalgae meal (Algae0, Algae50, Algae100, and Algae150, respectively). Steaks were displayed under simulated retail conditions for 7 d and percent metmyoglobin was calculated using the equations of Krzywicki (1979). T, treatment effect; R, linear effect of algae; Q, quadratic effect of algae; *significant effect ($P \leq 0.05$); *tendency ($P \leq 0.10$). (b) Data adapted from Phelps et al. (2017). Finishing steers fed a conventional feedlot finishing diet (CON), supplemental 100 g/steer $\cdot$ d $^{-1}$ DHA-rich microalgae (ALGAE), supplemental at 100 g/steer $\cdot$ d $^{-1}$ DHA-rich microalgae and antioxidant (vitamin E 103 IU/d and Sel-Plex; AOX), and supplemental 100 g/steer $\cdot$ d $^{-1}$ DHA-rich microalgae and antioxidant (vitamin E 103 IU/d and Sel-Plex) for the final 10 d of finishing (LATE).

studies reported pork loin is primarily composed of type IIX and IIB (glycolytic) fibers (Paulk et al., 2014; Noel et al., 2016), while other studies demonstrated beef was largely comprised of type I and IIA (oxidative) fibers (Phelps et al., 2014, 2016a). The fact that pork muscle possesses greater glycolytic metabolism could be the reason oxidation catalyzed discoloration is not as big of a factor; however, this topic requires more attention.

Mitigating color issues

Vitamin E or α -tocopherol has been identified as the major fat-soluble antioxidant that prevents oxidation in meat products (Wood and Enser, 1997). Grass-fed beef which has increased amounts of PUFA when compared with grain-fed beef also contains elevated levels of vitamin E, preventing excess oxidation of those FA (Daley et al., 2010). Research is limited on antioxidant inclusion in diets that also contain sources of PUFA such as flaxseed, fish oil/meal, or marine algae. While Albertí et al. (2014) found no color advantages when adding vitamin E to diets containing 5% flaxseed, Juárez et al. (2012) reported adding of vitamin E (1,051 IU/d) to diets of feedlot steers containing 10% flaxseed produced steaks with reduced calculated hue angle (less metmyoglobin) compared with steaks from cattle fed diets with 10% flaxseed and 451 IU/d vitamin E. At day 10 of retail display, Phelps et al. (2017) found supplementing selenium yeast and extra vitamin E in feedlot diets containing microalgae meal produced steaks with 40% greater a^* values than diets that did not contain antioxidants. Additionally, surface metmyoglobin percentage was decreased for steaks from steers fed antioxidants along with microalgae compared with steaks from steer only fed microalgae (Figure 2b). In pork, Gonzalez et al. (2019) hypothesized that elevated vitamin E content of the LIPEX feeding regimen was responsible for lack of detrimental color effects seen when elevating the omega-3 FA content of the LM. Overall, the management of color problems associated with altering the FA profile of meat products can be done by the use of antioxidants.

Effect of altering fatty acid profile on fresh meat palatability

Palatability of meats is broadly described as being the combined perception of tenderness, juiciness, and flavor (Bray, 1966). Tenderness has most frequently been identified as the greatest influencer of meat palatability (Savell et al., 1987; Müller et al., 1995). More recently, with improvements to meat tenderness, flavor was acknowledged as being the primary driver of meat palatability (Huffman et al., 1996; Corbin et al., 2015). Few studies have evaluated the importance of juiciness, in comparison to tenderness and flavor; however, multiple objective measures of juiciness are correlated with consumer overall liking, indicating some contribution of juiciness to palatability (Lucher et al., 2017). A compilation of 1,800 consumer responses determined tenderness, juiciness, and flavor each contribute to overall palatability, at 43.4%, 7.4%, and 49.4%, respectively (O'Quinn et al., 2018).

There are multiple contributors to perceived meat tenderness, namely actomyosin effects, amount and state of collagen, and lubrication effects from moisture and intramuscular fat (Smith and Carpenter, 1974). Juiciness is described as being the combination of initial fluid release and sustained flow of juices in response to fat (Weir, 1960). Flavor is the complex interaction of nonvolatile compounds interacting with receptors on the tongue and volatile compounds interacting with receptors within the oral-nasal cavity. For meats, flavor compounds are derived from the breakdown of protein and lipid components, followed by subsequent thermal lipid oxidation and the

Maillard reaction during cooking (Mottram, 1998). These brief descriptions of biochemical factors in relation to tenderness, juiciness, and flavor reveal a common theme. Intramuscular fat makes key contributions to each attribute. This contribution is supported by consumer response across fat content. For beef, both palatability score and the probability of an acceptable rating increased in response to increased intramuscular fat content (O'Quinn et al., 2018). In general terms, as total fat increased so do the positive perceptions of tenderness, juiciness, and flavor.

The results described above strongly support the contribution of overall fat content to palatability; however, greater insight may be drawn through evaluation of the fatty acids that make up a large majority of total lipids. Other than making up a large proportion of total lipids, fatty acids are variable in length and number of double bonds. Variation in these molecular features influence melting point, susceptibility to oxidation during storage, and thermal degradation during cooking. Each of these characteristics may ultimately influence palatability. Overall, there are two primary lipid categories that contain fatty acids, nonpolar triglycerides, and polar phospholipid groups. Overall, polar lipid fatty acids are less saturated, contain more fluid, and more susceptible to oxidation.

Numerous studies have considered the contributions of fatty acids to palatability and meat quality (Elmore et al., 2005; Scollan et al., 2006; Wood et al., 2008; Hunt et al., 2016). One common approach used to evaluate fatty acids is to categorize a large group of fatty acids into saturation categories (i.e., SFA, MUFA, and PUFA). Each of these categories, and the fatty acids which make them up, will vary with normal animal production factors. For young market beef, as time-on-feed and animal maturity increase intramuscular fat content also increases. As intramuscular fat increases, the overall fatty acid composition is altered. Biohydrogenation in the rumen leads to the preferential accumulation of SFA and MUFA. As a result, proportions of PUFA decrease over time while SFA and MUFA increase (Smet et al., 2004; Stelzleni and Johnson, 2008). Numerous studies demonstrated dietary components influence fatty acid content and composition (Noci et al., 2007; Duckett et al., 2009; Chail et al., 2016). For monogastric swine, diet is paramount to fatty acid make up of pork (Romans et al., 1995a; Wiseman and Agunbiade, 1998).

Variation in fatty acids may ultimately influence palatability. Oleic acid and cumulative MUFA are positively correlated with consumer flavor liking, juiciness, tenderness, and overall liking (Hwang and Joo, 2017). Furthermore, O'Quinn et al. (2016) positively correlated MUFA with beefy/brothy, browned/grilled, buttery/beef fat, nutty, sweet, and overall flavor desirability; attributes considered desirable flavor attributes. Conversely, MUFA was negatively correlated with undesirable attributes, bloody/metallic, gamey, livery, fishy, and sour. These results imply that MUFA and the predominate MUFA, oleic acid, are related with good eating experiences, in agreement with other works (Dryden and Maechello, 1970; Westerling and Hedrick, 1979).

In contrast, stearic acid and n -3 fatty acids were each negatively correlated to overall liking and the previously described desirable attributes (O'Quinn et al., 2016; Hwang and Joo, 2017). These results imply that stearic acid and n -3 fatty acids are related with undesirable eating attributes and poor palatability, which are comparable with other early studies (Westerling and Hedrick, 1979; Melton et al., 1982).

Meat with greater intramuscular fat content have greater oleic acid and MUFA content compared with leaner meat. Meanwhile, meat with greater intramuscular fat content tends

to have lower proportions of stearic acid and *n*-3 fatty acids. Therefore, it is unclear if oleic acid and MUFA directly influence positive eating experiences or if greater overall intramuscular fat imparts the desirable eating experience. Likewise, it is unclear if less desirable palatability is due to stearic acid and *n*-3 fatty acids proportion of leaner meat.

However, the impact of lipid oxidation on eating experience is clearer. When lipid oxidation occurs beyond acceptable levels, palatability is diminished; therefore, any changes to fatty acids which may influence lipid oxidation is of interest for palatability. When proportions of fatty acids shift to being less saturated, there is a greater potential for lipid oxidation. Specifically, greater *n*-3 fatty acids are more susceptible to lipid oxidation. In comparison with other PUFA, primarily *n*-6, *n*-3 fatty acids have a greater overall number of double bonds and thus greater likelihood for lipid oxidation. Oxidation of *n*-3 fatty acids and subsequent decreases in organoleptic appeal have been outlined before (Romeu-Nadal et al., 2007; Arab-Tehrany et al., 2012). Kouba et al. (2003) comprehensively demonstrated the impacts of increasing *n*-3 fatty acids in pork. Through feeding of linseed, both linolenic acid (18:3n3) and eicosapentaenoic acid (20:5n3) were increased. The increase in these *n*-3 fatty acids was implicated in decreases in positive pork odor, pork flavor, and overall flavor liking. The authors also outlined increased lipid oxidation through the measurement of Thiobarbituric acid reactive substances (TBARS).

For consumers, perception of lipid oxidation occurs through the detection of volatile compounds. Specifically, oxidation of PUFA yielded numerous volatile aldehydes, alcohols, furans, and ketones (Frankel, 1991). These volatile products of lipid oxidation are demonstrated to be expressed more prominently in lean meats (Legako et al., 2015a, 2016). The expression of volatile compounds in leaner meat may be the result of overall lipid proportions. Polar phospholipids are more likely to be oxidized in comparison to the neutral lipid triglycerides (Mottram, 1998). Leaner meats have a greater proportion of polar lipids in comparison to meats with greater intramuscular fat content (Wood et al., 2008; Legako et al., 2015b). Polar lipids are also known to be less saturated in comparison to neutral lipids. Volatile compounds derived from lipid oxidation increase as much as 4-fold when the proportion of PUFA is increased (Elmore et al., 1999). In summary, leaner meats will possess a greater proportion of polar lipids which have a greater proportion of PUFA known to be highly susceptible to lipid oxidation. As a result, volatile compounds originating from lipid oxidation are expressed more greatly in lean meats. The impact of this is lower flavor liking and decreased palatability overall.

Alteration of fatty acids in meats can occur through accumulation of intramuscular fat. Overwhelming evidence exists to say greater intramuscular fat content is positive for palatability. It is evident in beef that increased intramuscular fat lends to decreased proportions of *n*-3 fatty acids. Greater proportions of *n*-3 fatty acids are highly likely to increase the degree of lipid oxidation in meats. In leaner meats, there is an inherently greater level of unsaturation among fatty acids, thus an inherently greater potential for lipid oxidation. Taken all of this as a whole, alteration of fatty acids toward a lower degree of oxidation would be beneficial for flavor and overall palatability. Furthermore, greater intramuscular fat content lends itself to imparting greater juiciness and tenderness.

Conclusion

Innovative strategies to alter adipose tissue depot composition en masse or in a targeted fashion are the next frontier in meat

animal agriculture and One Health biomedicine. This highlights the integral role adipose tissue plays in livestock physiology, productivity, and profitability. Modification of pork product composition can be done with relative predictability (Paulk et al., 2015), while beef products require more indirect approaches to account for microbial metabolism. As the rumen microbiome comes into focus, it may become more feasible to manage exogenous lipid metabolism according to the demographics of the resident microflora and use their subsequent metabolism to modify tissue composition. For example, studies in cattle suggest that the rumen microbiome is moderately heritable (Myer, 2019) and can be used to predict FA composition of milk products. Coupling genetic information with rumen microbiome data improved the predictive value for odd chain and PUFA in Holstein milk (Buitenhuis et al., 2019). Applying these principles to FA composition of other adipose tissue depots in beef and other ruminant animals has the potential to increase the consistency and profitability of meat production through increased compositional quality. An improved understanding of adipose physiology in contemporary production scenarios will potentiate these precision meat production practices that satisfy both the physiology of the animal and compositional preferences of the consumer in an efficient manner.

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Conflict of interest statement

The authors declare no conflict of interest.

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