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MEAT SCIENCE

The qualities of meat — its composition, nutritional value, wholesomeness and consumer acceptability — are largely determined by the events and conditions encountered by the embryo, the live animal and the post-mortem musculature. The control of these qualities, and their further enhancement, are thus dependent on a fuller understanding of the commodity at all stages of its existence — from the initial conception, growth and development of the organism to the time of slaughter and to the ultimate processing, distribution, preparation, cooking and consumption of its meat.

It is the purpose of *Meat Science* to provide an appropriate medium for the dissemination of interdisciplinary and international knowledge on all the factors which influence the properties of meat. The journal is predominantly concerned with the flesh of mammals; however, contributions on poultry meat may be published, especially if these have relevance to our overall understanding of the relationship between the nature of muscle and the quality of the meat which muscles become post mortem.

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A fresh look at meat flavor

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Abstract

Hundreds of compounds contribute to the flavor and aroma of meat. Complex interactions between various compounds influence the perception of meat flavor. Inherent flavor of a meat product can be influenced by oxidation, lipid content, feeding/diet, myoglobin, and pH. Diet plays an important role in both ruminants and nonruminants. New research reveals important relationships in flavor among multiple muscles within a single animal carcass. This animal effect includes the presence of off-flavors. Diets high in polyunsaturated fatty acids may be contributing to the appearance of off-flavors in beef. Compounds associated with liver-like off-flavor notes in beef have been identified in raw tissue.

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Keywords: Flavor; Meat; Beef; Off-flavor; Liver flavor

1. Importance of flavor to eating satisfaction

Flavor is a very complex attribute of meat palatability. The Beef Customer Satisfaction Survey found many factors that influenced overall like ratings of top round, top sirloin, and top loin steaks with flavor and tenderness contributing equally to overall like ratings (Lorenzen et al., 1999; Neely et al., 1998; Neely et al., 1999; Savell et al., 1999). For clod steaks, flavor like had the largest simple correlation (0.86) to overall like ratings and was the first variable to enter the stepwise regression for predicting overall like rating (Goodson et al., 2002).

While it has been known for many years that tenderness plays a large role in acceptability of meat by a consumer, it has become increasingly apparent that flavor also needs to be addressed. In a large, multiple-city study, flavor was found to be the most important factor affecting consumers' meat buying habits and preferences when tenderness was held constant (Sitz, Calkins, Feuz, Umberger, & Eskridge, 2005). Huffman et al. (1996) found flavor had a stronger relationship ($R^2 = 0.67$) to overall steak palatability ratings

than any other factor when consumers prepared meat at home. Platter et al. (2003) determined that small changes in sensory ratings for flavor greatly influenced the overall acceptability of steaks.

Because of the relationship of flavor to meat palatability it is important to gain a better understanding of factors that influence flavor in order to produce the most flavorful and consistent product possible.

2. Basic flavor compounds formed upon cooking

There are literally hundreds of compounds in meat that contribute to flavor and aroma. Many of them are altered through storage and cooking, making meat flavor an incredibly complex topic. Entire books have been written on individual aspects of meat flavor. The intent of this paper is to highlight some of the major flavor compounds and to discuss a unique flavor problem with global implications currently facing beef producers in the US. The primary focus of this paper is the inherent flavor of meat. That is, little attention will be given to post-cooking flavor changes (like the development of warmed-over flavor).

Flavor and aroma compounds found in meat (Table 1) include a broad array of compounds, including hydrocar-

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Table 1

Compounds identified in beef and characteristic flavors and/or aromas associated with those compounds

Compound name	Characteristic flavors/aromas
Benzaldehyde	Volatile almond oil, bitter almond, burning aromatic taste
Benzene	Pleasant, distinct
sec-Butanamine	Seafood, green, onion
Butenal	Malty, green, roast
n-Capric acid	Goaty
3-Carene	Sweet and pungent odor but more agreeable than turpentine, orange peel, lemon, resin
Cyclobutanol	Roasted
2,2,6-Trimethylcyclohexanone	Mint, acetone
2,4-Decadienal	Deep fat flavor, chicken flavor at 10 ppm, citrus/orange/grapefruit flavor at lower dilutions
Decanal	Powerful, waxy, aldehydic, orange, citrus peel
2-Decenal	Tallow, orange
1,3-Bis(1,1-dimethylethyl)benzene	Cooked beef
2,3-Dimethyloxirane	No reference
N,N'-Dimethyl 1,2-ethanediamine	Ammonia
5-Ethylcyclopent-1-enecarboxaldehyde	Fragrant, perfume
2-Pentylfuran	Green bean, butter
2,4-Heptadienal	Nut, fat
Heptanal	Oily, fatty, rancid, unpleasant, penetrating fruity odor in liquid
5-Methyl 2-heptanamine	No reference
1-Heptanol	Fragrant, woody, oily, green, fatty, winey, sap, herb
2-Heptanone	Fruity, spicy, cinnamon, penetrating fruity odor in liquid
6-Methyl 2-heptanone	Cloves, menthol, eugenol
2-Heptenal	Soapy, fatty, almond, fishy, unpleasant
3-Ethyl-2-methyl 1,3-hexadiene	No reference
Hexanal	Fatty-green, grassy, strong green, tallow, fat, unripe fruit when dilute
Hexane	Faint peculiar odor
Hexanol	Woody, cut grass, chemical-winey, fatty, fruity, weak metallic
2-Ethyl 1-hexanol	Resin, flower, green
2-Hexen-1-ol	Green, sharp, leafy, fruity, unripe banana
Hydroxymandelic acid	No reference; catecholamine metabolite
Limonene	Pleasant lemon-like, turpentine, citrus, fruity, fresh, light
Bis(2-trimethylsilyethyl ester) malonic acid	No reference
3-Methylbutanal	Pungent apple-like odor, malt
Methyl salicylate	Cooling sensation, wintergreen, gaultheria
2,4-Nonadienal	Fat, wax, green, watermelon, geranium, pungent
Nonanal	Floral, citrus, fatty, grassy, waxy, green
2-Nonanone	Hot milk, soap, green, fruity, floral
2-Nonenal	Cardboardy, orris, fat, cucumber, paper
Octadecanal	Oil
Octanal	Harsh, fatty, orange peel, soapy, lemon, green, honey
1-Octanol	Penetrating aromatic odor, fatty, waxy, citrus, oily, walnut, moss, chemical, metal, burnt
2-Methyl 3-octanone	Herb, butter, resin, gasoline
2-Octenal	Green, nut, fat
(Z)-3-Octene	Fruity, old apples
1-Octen-3-ol	Mushrooms, compound excreted by many insects
2-Octen-1-ol	Green citrus
3-Octen-2-one	Nut, crushed bug, earthy, spicy, herbal, sweet, mushroom, hay, blueberry
Hexadecyl oxirane	No reference
Pentanal	Almond, malt, pungent, acrid
Pentane	Very slight warmed-over flavor, oxidized
1-Pentanol	Mild odor, fusel oil, fruit, balsamic
5-Amino 1-pentanol	Mild
α -Pinene	Piney, fruity, citrus, turpentine
β -Pinene	Pine, citrus, fruity, resin, turpentine
Piperazine	Salty
N-Methyl 1,3-propanediamine	No reference
Propanol	Alcoholic
Styrene	Penetrating odor, sweet smell
Tetradecane	Alkane
Tridecane	Alkane
2-Tridecenal	Sweet, strong, spicy
Undec-4-enal	No reference; animal pheromone

bons, aldehydes, ketones, alcohols, furans, triphenes, pyrrols, pyridines, pyrazines, oxazols, thiazols, sulfurous compounds, and many others (MacLeod, 1994; Ho, Oh, & Bae-Lee, 1994). A few of the key reactions will be discussed below.

2.1. Maillard reaction

The Maillard reaction, or nonenzymatic browning, helps explain amine and carbonyl reactions in food. In general, amino compounds condense with the carbonyl group of a reducing sugar in the presence of heat. This produces glycosylamine which is rearranged and dehydrated to form furfural, furanone derivatives, hydroxyketones, and dicarbonyl compounds. All of these compounds contribute to flavor. As the reaction progresses, the intermediates can react with other amines, amino acids, aldehydes, hydrogen sulfide, and ammonia through the Amadori rearrangement, Strecker degradation, and Schiff bases pathways.

Once the reaction has progressed through the Schiff base, Strecker degradation, or other pathways, the reactions can lead to melanoidins (brown, high molecular weight polymers from the condensation of cyclic compounds) (Fay & Brevard, 2005). These products can be pleasing or unacceptable flavors and aromas (Manley & Choudhury, 1999).

Different sugars and amino groups can produce different end products. Cysteine and glucose produce mainly sulfur compounds whereas cysteine and glucose under oxidized conditions produce more pyrazines and furans (Tai & Ho, 1997). Maillard volatile compounds from glutathione and glucose produce sulfur-containing compounds – thiophenes, thiazoles, and cyclic polysulfides – at pH 6 and 8, but furans are more often the end products at more acidic pH. When glutathione is oxidized it becomes glutathionesulfonic acid, which produces furans, carbonyls, pyrroles, and pyrazines with glucose. Sulfur-containing compounds are not formed when glutathione is oxidized (Tai & Ho, 1998).

Cysteine and ribose, through the Maillard reaction, as well as thiamin have been shown to create compounds such as 2-methyl-3-furanthiol (Mottram & Whitfield, 1994). From these compounds thiols and disulfides can originate.

An exhaustive review of the nine most common aromatic compound classes from precursors of the Maillard reaction can be found in Manley and Choudhury (1999). However, more extensive research is needed to determine the role of each amino acid and sugar in meat to create the browned, cooked meat flavor. It would be useful to know if there are differences among muscles, cooking methods, and degrees of doneness, and how these differences affect the end flavor profile.

2.2. Flavor compounds

Sulfurous and carbonyl compounds seem to be the predominant contributor to meat flavor (Mottram & Mad-

ruga, 1994; Shahidi, 1989). Gasser and Grosch (1988) established that 2-methyl-3-furanthiol and bis(2-methyl-3-furyl) disulfide contribute to the desirable aroma of beef when isolated from other possible compounds contributing to meat aroma. Bis(2-methyl-3-furyl) has an odor threshold of 0.02 ng/g in water and methylating 2-methyl-3-furanthiol increases the odor threshold. This suggests 2-methyl-3-(methylthio)furan is only a minor contributor to the flavor of meat (MacLeod, 1986). Gasser and Grosch (1988) also established flavor dilution factors (FD; aroma extracts are stepwise diluted until sniffers cannot detect odorants with the highest level reported as flavor dilution) to evaluate the contribution of a compound to overall beef flavor. Forty compounds were determined in cooked beef to have FD factors larger than four, and 17 compounds, which were stated to be major contributors to cooked flavor, had FD factors larger than 64. Farmer and Patterson (1991) isolated five compounds that were found to be desirable to cooked beef flavor: bis(2-methyl-3-furyl) disulfide, 2-furfuryl 2-methyl-3-furyl disulfide, bis(2-furfuryl) disulfide, dimethylfuryl 2-methyl-3-furyl disulfide, 2-methyl-3-furyl 2-methyl-3-thienyl disulfide.

A Strecker aldehyde, methional, is a low threshold (0.2 µg/g in water) sulfur compound that is described as ‘pleasant, warm-meat, or soup-like’ (Gasser & Grosch, 1988). The roasty note in beef is in part produced by 2-acetyl-1-pyrroline and 2-acetylthiazole.

Many compounds that contribute to meat smell and flavor are lipid breakdown products. Fatty acids such as linoleic and arachidonic acid start to autoxidize to 9-hydroperoxide and 11-hydroperoxide, respectively, which can form 2,4-decadienal, 2-nonenal, 1-octen-3-one, 2,4-nonadienal, and 2-octenal through β -scission with 2-nonenal and 2,4-decadienal having as high of FD values as the sulfur compounds contributing to meaty flavor.

Through oxidation of β -carotene, a very intense aromatic β -ionone is formed (Sanderson, Co, & Gonzalez, 1971) which likely comes from animal feed (Gasser & Grosch, 1988). One compound responsible for the tallowy and/or beef-like smell is 12-methyltridecanal (Guth & Grosch, 1993), a compound derived from plasmalogens, glycerophospholipids with a long chain fatty aldehyde linked to the *sn*-1 position by a vinyl ester bond (Dannenberg et al., 2006; Guth & Grosch, 1993). The 12-methyltridecanal’s odor threshold is 0.1 µg/kg in water and the compound is found in higher amounts in lean from beef than other species (Guth & Grosch, 1993). Increasing the amount of forage in the diet of cattle increases 12-methyltridecanal in the phospholipids of muscles as well as *n*-octadecanal, another plasmalogen. Octadecanal, a mono-unsaturated plasmalogen with a low odor threshold, was reduced when forages were fed instead of concentrates, but *n*-hexadecanal concentration was not affected by diet (Dannenberg et al., 2006).

Hexanal and 2,4-decadienal contribute positively to beef flavor, but may produce undesirable flavors at higher concentrations (Melton, 1983). This is probably because these

two compounds are produced in the greatest amounts during oxidation of 18:2 during heating as well as overshadowing of compounds that also help produce typical beef flavors. Others have found that hexanal is the most prominent volatile compound in cooked meat with the amount being directly proportional to thiobarbituric acid reactive substances (TBARS), a measure of oxidation, and inversely proportional to flavor acceptability (Shahidi & Pegg, 1994; Ullrich & Grosch, 1987).

2.3. Species differences in fatty acid deposition

Because of differences in digestive systems between ruminants and nonruminants, deposition of fatty acids is different. Poultry and pork muscle typically have higher levels of polyunsaturated fatty acids than lamb or beef. Pork muscle has more linoleic acid than beef or lamb which contributes to the higher polyunsaturated:saturated fatty acid ratio. However, beef and lamb commonly have more favorable *n*6:*n*3 fatty acids ratios than pork (Wood & Enser, 1997). Through diet manipulation some change in the fatty acid composition can be achieved. Since dietary polyunsaturated fatty acids undergo little change during digestion in pork and poultry, feeding products with higher levels of linolenic, eicosapentaenoic, and docosahexaenoic has been studied to modify the *n*-6 concentration of fatty acids in those species.

Modifying the levels of unsaturated fatty acids in pork and poultry has led to conflicting reports on the effect on flavor. Rhee, Davidson, Cross, and Ziprin (1990) found all taste panel palatability scores for pork improved as oleic acid concentration increased. Myer et al. (1992) found feeding high oleic acid peanuts to pigs did not affect taste panel scores for flavor. However, they did see an increase in off-flavor scores when canola oil was fed at levels where the content of linolenic was raised fivefold in subcutaneous fat. Shackelford, Reagan, Haydon, and Miller (1990) also found off-flavors increased with feeding canola oil to pigs, compared with other high oleic acid dietary products, which they attributed to the increase in 2-pentenal and 2,4-heptandienal, derivatives of linolenic acid. Based on these studies it appears raising monounsaturated fatty acids does not lead to the negative flavor profile that is seen by increases in polyunsaturated fatty acids in pork.

Wood and Enser (1997) reviewed factors influencing fatty acids in meat and their effect on quality and concluded that poultry and pork respond similarly when trying to manipulate the *n*6:*n*3 fatty acid ratio. Increases in *n*3 fatty acids in bacon, like those found when feeding fish oil (eicosapentaenoic acid and docosahexaenoic acid), lead to increases in perception of off-flavors by taste panelists. This trend was not seen for the pork loin (Romans, Johnson, Wulf, Libal, & Costello, 1995; Romans, Wulf, Johnson, Libal, & Costello, 1995).

Camfield, Brown, Lewis, Rakes, and Johnson (1997) presented simple correlations of medium and long chain fatty acids to specific flavors and concluded unsaturated

fatty acids were positively correlated to cowy, cardboard, painty, and livery flavors that are unsatisfactory for beef palatability.

Differences in production systems create contradictory findings in the relationship of fatty acid type and concentration to flavor. Some studies have shown flavor differences when beef cattle are fed forage- and cereal-based diets (Mandell, Buchanan-Smith, & Campbell, 1998; Melton, 1990; Raes et al., 2003; Young & Baumeister, 1999). In one review, it was concluded flavor differences could not be reliably determined (Muir, Deaker, & Brown, 2003). There are many reasons for the discrepancies in these studies. Consumer preferences and animal management systems vary greatly, as do the amount of grain/concentrate and type of forage used for comparison. Several studies have investigated breed effects, age of the animal, estimated fat cover end point, or supplements, all of which could impact the fatty acid profile of fat deposits. Studies with USA consumers demonstrate they prefer meat from grain-finished beef (Killinger, Calkins, Umberger, Feuz, & Eskridge, 2004; Sitz et al., 2005). However, those same studies revealed a small sector of the US population that prefers the flavor and palatability of steaks from grass-finished animals. This split preference for meat from different production systems is probably true in many countries. In general, grass-fed and grain-fed ruminant animals have been shown to have different fatty acid profiles with grass-fed animals having higher levels of polyunsaturated fatty acids, especially linolenic acid and other *n*-3 fatty acids, while concentrate-fed animals contain higher levels of *n*-6 fatty acids and a lower proportion of *n*-3 fatty acids.

3. Effect of fat, lipid content and oxidation on flavor

3.1. Fat and lipid content

It is commonly known that the degree of lipid oxidation in meat is dependent on the composition of the phospholipids, amount of polyunsaturated fatty acids, and the concentrations of metal ions, oxygen, salt and other pro-oxidants. Peroxides are formed by the free radical chain mechanism between a polyunsaturated fatty acid and oxygen. This oxidation forms products like aldehydes, lactones, hydrocarbons, furans, and ketones that create undesirable, rancid off-flavors due to the oxidation of meat (Ladikos & Lougovois, 1990).

Oxidation can be controlled by the amount of antioxidant compounds found in the muscle tissue. Grass-fed beef may not be much more prone to lipid oxidation than grain-fed beef because of the increased levels of vitamins A, C, and E, carotenoids, and flavonoids found in forages (Wood & Enser, 1997). Grain-fed animals also consume polyphenols or may be fed vitamin E supplements during the finishing period which act as antioxidants.

Lipids serve several roles in flavor development. Lipids in meat act as a solvent for the volatile compounds that develop during production, handling, and thermal process-

ing (Moody, 1983). They undergo thermal oxidative change to produce compounds that influence beef flavor and react with components of lean tissue to give distinct flavor compounds (Mottram & Edwards, 1983).

Correlations between 14:1, 16:1, 18:0, 18:1, 18:2, 18:3, and desirable beef flavor have been reported (Melton, Black, Davis, & Backus, 1982). Although species flavor depends primarily on unsaturated aldehydes, fatty acids, ketones, and saturated aldehydes all play a role in beef flavor – especially since many of the aldehydes are derived from pathways with fatty acids (Melton et al., 1982).

Fat content has been shown to affect palatability, including flavor. As intramuscular fat increases, the fat flavor increases which is preferred by most US consumers (Miller, Moeller, Goodwin, Lorenzen, & Savell, 2000). The minimal level of intramuscular fat in beef for US consumer acceptance and preference, described as slightly intense fat flavor, is approximately 3% (Miller, 2001). Levels of fat above 7.3% in meat may have a negative effect on perception of flavor and acceptability (Miller, 2001). Francis, Romans, and Norton (1977) also found a bell-shaped curve for the effect of marbling on flavor. Conversely, loin steaks had a linear decrease in flavor desirability as quality grade went down from USDA Prime through USDA Cutter (Smith, Savell, Cross, & Carpenter, 1983). Flavor desirability ratings in top round steak were less affected by grade and marbling score.

3.2. Oxidation and volatiles from fatty acids

To determine the volatile compounds that are derived from linoleic acid and methyl linoleate, Ullrich and Grosch (1987) used gas chromatography to derive a *D*-value (the highest dilution at which the aroma of a substance is still detected) to reveal the most intense flavor compounds. With both lipids, hexanal, 2-octenal, and 2-nonenal had the highest *D*-values. The fourth highest compound for linoleic acid was 1-octen-3-ol while 1-octen-3-one was for methyl linoleate. After 24 h of linoleic autoxidation, 2-nonenal was the most potent volatile, with hexanal the most potent volatile after 48 h, and hexanal and 2-octenal the most potent volatiles after 72 h. The authors also found pentane to be a better indicator of lipid peroxidation because it has a shorter induction period than other volatile compounds even though its *D*-value is not as high.

Arachidonic acid, a long chain omega-6 polyunsaturated fatty acid, was originally found to be autoxidized in meat into hexanal, methyl 5-oxopentanoate, pentane, and 2,4-decadienal volatile compounds (Artz, Perkins, & Salvador-Henson, 1993). However, the most intense aroma compound from the oxidation of arachidonic acid is *trans*-4,5-epoxy-(*E*)-2-decenal followed by 1-octen-3-one, 2,4-decadienal, 2,4,7-tridecatrinal, and hexanal (Blank, Lin, Vera, Welti, & Fay, 2001).

For human health reasons, there is a desire to increase the PUFA in the lean portion of meat. However, when lev-

els become too high, off-flavors can develop, especially during cooking (Elmore, Campo, Enser, & Mottram, 2002).

4. Effect of diet on flavor

4.1. Flavor intensity

The primary focus on the effect of diet and flavor acceptability has been comparing pasture-fed cattle to grain-fed cattle. A wide range of results have been reported: some papers suggest there are no differences between forage-fed and grain-fed animals and others stating there are large differences. Most of the differences can probably be explained by the different production systems which affect the level of energy intake, days on feed, growth rate, age of the animal, fat deposition, fat composition, and carcass weight. Brown, Melton, Riemann, and Backus (1979) stated sensory panels do not find a lack of flavor in grass-fed beef, 'but rather the presence of an off-flavor.'

4.2. Lipid deposition and fatty acid oxidation

Compared to same-age steers fed corn silage-, pasture-, and Bermuda pellets, steers finished 90 d on high energy, corn-based diets had more desirable or intense beef flavor (Melton, 1983). When feeding to a constant fat thickness in different production management systems, flavor differences existed (Bowling et al., 1978). Even when comparing corn diets to corn silage diets, significant differences were seen in flavor profiles of beef, although not to the extent of grass or alfalfa finished steers (Berry, Leddy, Bond, Rumsey, & Hammond, 1988). Conversely, no difference in flavor was seen between the grass- and grain-fed animals when animals were blocked by growth rate (French et al., 2001). The high growth rate animals fed on grass had little difference in meat quality to concentrate-fed cattle which the authors attributed to high protein turnover (French et al., 2001). Global differences in flavor preference may partially explain the latter result.

Several grasses in ruminant diets have been demonstrated to cause less desirable meat flavor (Melton, 1990). In contrast, Bidner, Montgomery, Bagley, and McMillin (1985) found no difference in flavor intensity in meat from animals fed high quality Bermuda grass pasture compared to corn-based diets. French, O'Riordan, et al. (2000) reported no differences in flavor after aging the meat 2 d when steers were finished on autumn grass, grass silage, or concentrate diets with low levels of supplements to maintain constant carcass growth rate between treatments. Melton (1983) suggested differences in results could be due to differences in sensory panels or quality of the grasses.

Hay diets were also found to produce meat less desirable in flavor than corn silage diets with no direct link to intramuscular fat (Dube et al., 1971), while another study showed the opposite effect (meat from animals on a 91% corn diet were less desirable in flavor than meat from animals fed alfalfa or Timothy hay) when using hay as the

energy source (Oltjen, Rumsey, & Putnam, 1971). Furthermore, hay versus grass silage diets fed at the same net energy do not affect flavor (Listrat et al., 1999). Melton (1983) concluded corn could be replaced partially or totally with high quality alfalfa or in combination with Timothy hay without a significant change in flavor.

Corn is the staple grain used in grain-fed cattle in the US while Canada and Japan predominately use barley. Sitz et al. (2005) and Jeremiah et al. (1998) found US consumers preferred the flavor of domestic beef over Canadian barley-fed beef. In contrast, no differences in flavor intensity, 12 aromatics, two mouthfeels (astringent and metallic), and three tastes – as determined by a trained flavor and descriptive panel – were found when comparing corn, barley, and 50–50 corn/barley diets in the meat from young animals (Miller, Rockwell, Lunt, & Carstens, 1996).

The majority of the flavor effect due to feeding of forages is hypothesized to be due to changes in lipid deposition and fatty acid composition. Using sheep as a ruminant model, Lee et al. (2004) hypothesized red clover fed to grass-finished steers would increase both *n*-6 and *n*-3 polyunsaturated fatty acids (PUFA) due to reductions in ruminal biohydrogenation of PUFA. French, Stanton, et al. (2000) found meat from cattle that were grass supplemented to maintain constant growth rate with concentrate-fed animals had a linear decrease in saturated fats and *n*-6:*n*-3 PUFA ratios and increases in unsaturated fats and conjugated linoleic acid (CLA) when concentrate percentage went down, without affecting flavor scores (French, O'Riordan, et al., 2000). Fishy off-flavor was significantly higher and overall flavor liking scores were significantly lower in meat from grass-finished cattle with increased 18:1 *trans* isomers and, notably, CLA_{cis}-9, *trans*-11 (Nuernberg et al., 2005). Animals backgrounded on grass and then finished approximately 190 d on a high energy diet of silage, hay, and barley had meat with higher levels of *n*-3 fatty acids than animals fed concentrate after weaning, but no difference in CLA_{cis}-9, *trans*-11 in the lipids of the longissimus muscle (Dannenberger et al., 2004) and subcutaneous fat (Dannenberger et al., 2005). However, CLA_{trans}-7, *cis*-9 was the second most abundant CLA isomer in meat from concentrate-fed animals whereas CLA_{trans}-11, *cis*-13 was the second most abundant in grass-fed. Total CLA isomers were increased in the longissimus, subcutaneous fat, heart, and liver, but not in the semitendinosus (Dannenberger et al., 2005) in grass-fed animals. Most importantly, this study showed Δ^9 -desaturase activity was decreased due to pasture feeding. This elongase, in conjunction with *trans* vaccenic acid, is responsible for the synthesis of CLA_{cis}-9, *trans*-11. By disrupting the elongase activity, flavor changes might occur because of the unused *trans* vaccenic acid, a fatty acid implicated in off-flavors (Camfield et al., 1997) as well as less CLA_{cis}-9, *trans*-11 (Dannenberger et al., 2005). French, Stanton, et al. (2000) also hypothesized the increase in CLA_{cis}-9, *trans*-11 in animals on higher grass-based diets was due to a change in biohydrogenation. However, they concluded

grass diets favored the growth of *Butyrivibrio fibrisolvens*, the ruminal bacterium responsible for producing the linoleic acid isomerase.

With interest to increase the PUFA in beef, trials with supplements high in certain fatty acids have been conducted. Most attempts have been made using linseed, linseed oil, sunflower, sunflower oil, and fish oil (Mandell, Buchanan-Smith, Holub, & Campbell, 1997; Scollan et al., 2006). Generally, levels of PUFA in the lean have not been high enough to claim health benefits, but some negative flavors due to oxidation and shorter shelf-life have been reported (Miller, 2001). The long chain fatty acids in fish oil (Richardson et al., 2004) and several long chain fatty acids from plant oils can bypass rumen biohydrogenation with minimal change (Scollan et al., 2004). This increase in unsaturation can lead to negative flavor perception.

After 80–90 d on a corn finishing diet, no further significant beef flavor changes occur (Melton et al., 1982). Liver flavor intensity increased up to 86 d of corn-based diets, and sour flavor intensity decreased to a minimum at 122 d on corn, while metallic and off-flavor intensity were unaffected by time-on-feed. Fishy and milky-oily flavors decreased linearly with time-on-feed. Melton et al. (1982) hypothesized increased beef fat and liver flavor with decreased milky-oily, sour and fishy flavor gave a more desirable beef flavor in corn-fed beef. Mandell et al. (1998) disagreed with this hypothesis as they found liver flavor was positively correlated to metallic and grassy aroma, sour flavor, and metallic and grassy aftertaste and negatively correlated to beef flavor. They also found sour flavor notes were not affected by production type, but metallic aroma was affected due to the differences in 18:1 and 18:3 in the meat from the different feed sources.

The biggest difference in the flavor of meat from grass- and grain-fed beef animals probably is due to fatty acid concentration and type as fatty acids are the primary source of carbonyl compounds (Melton, 1983). Oleic and linoleic acid are found in higher concentrations in grain-fed diets than in grass-fed diets (Enser et al., 1998; Vasta & Priolo, 2006) while α -linolenic is higher in grass-based diets (Enser et al., 1998). Therefore, compounds which are derived from linolenic acid (4-heptenal, 2,4-heptadienal, and 2,6-nonadienal) are usually in higher concentration in meat from grass-fed animals while hexanal, 2-heptenal, and 2,4-decadienal (products of linoleic acid) are typically found in higher concentrations in meat from grain-fed animals (Larick et al., 1987). Those compounds have been shown to be higher in beef with higher levels of oxidation. Furthermore, beef from corn-based diets has higher levels of glucose (Brown et al., 1979; Melton et al., 1982), γ - and α -tocopherol (Yang, Lanari, Brewster, & Tume, 2002), and carotenoids (Melton, 1990; Yang et al., 2002).

It is important to note most of these findings on flavor were studied in the US. An individual usually comes to prefer the foods he/she grew up eating. Sitz et al. (2005) and

Killinger et al. (2004) found the greatest sensory difference between Australian or Argentine (respectively) grass-fed and USA grain-fed beef to be flavor when Warner-Bratzler Shear force values were kept constant. Canadian, barley-finished cattle were also rated less desirable for flavor than domestic beef (Sitz et al., 2005). However, 19% of the consumers in the study preferred the Australian meat when compared to domestic beef while 29.3% preferred the Canadian-fed beef when compared to domestic beef. Consumers in both studies were willing to pay a premium for their preference, which was heavily influenced by flavor.

4.3. Volatile compounds

Larick et al. (1987) investigated differences in volatile compounds in forage systems and grain-fed cattle. Fat from animals finished on tall fescue, brome grass-red clover versus orchard grass-red clover pastures were not different in volatile compounds, but 31 volatiles were in different concentration in the meat from grain-fed animals. Volatiles higher in the meat fat from grass-fed animals included pentanoic, heptanoic, octanoic, nonanoic, decanoic, and dodecanoic acids; heptanal, 2,3-octanedione, 3-hydroxy-octan-2-one, 2-decenal, 2-tridecanone, hexadecane, heptadecane, octadecane, δ -dodecalactone, phyt-1-ene, neophytadiene, phyt-2-ene, an isomer of neophytadiene, 2-heptadecanone, dihydrophytol, and phytol with the terpenoids in much higher concentration due to rumen-fermented chlorophyll (Suzuki & Bailey, 1985). The fat from the grain-produced animals was higher in δ -tetradecalactone and δ -hexadecalactone (Larick et al., 1987). These lactones are derived in the rumen by the oxidation of linoleic and oleic acids (Vasta & Priolo, 2006). In the study, Larick et al. (1987) found phyt-2-ene to be highly correlated to beef flavor intensity while δ -tetradecalactone and δ -hexadecalactone were negatively correlated to grassy flavor. Pentanal, toluene, 1-ethyl-2-methylbenzene, and an unknown compound explained 51% of the variation of beef fat flavor intensity between grass and grain finished (Melton, 1990). As days on feed increased, pentanal, hexanal, 4-methyl-3-penten-3-one, nonane, acetone, nonanal, and two unknown compounds increased while *trans*-3-octene, *cis*-2-octene, toluene, 3-penten-2-one, 3-hydroxy-2-butanone, and five unknown compounds decreased (Melton, 1990).

Several classes of compounds are affected by the animal's diet. Descalzo et al. (2005) found more aldehydes in meat from animals eating concentrate diets rather than grass. Phenolic compounds are secondary metabolites of plants so they are typically found in higher concentration in meat of forage-finished animals compared with grain-finished with the exception of 4-ethylphenol and cresols (Vasta & Priolo, 2006). Diet plays a large role on indoles and their derivatives with grass-fed animals having much higher levels, especially skatole. Production of these indoles from ruminal microorganisms can be reduced by feeding feedstuffs with higher levels of tannins for a few days

(Vasta & Priolo, 2006). The volatile 2,3-octanedione has been suggested as an indicator of grass-fed animals since the compound is produced by a lipoxygenase on leafy plants (not seeds) (Young, Berdague, Viallon, Roussett-Akrim, & Theriez, 1997) and soybeans (Elmore et al., 2004). This compound can also be derived from heating and breaking down linoleic acid (Elmore et al., 2002) so care is needed if using the compound as an indicator of grass-fed animals. Terpenoids are directly transferred from grass to animal tissue so these compounds are also considered a green forage indicator except for β -gurjunene and limonene, which are higher in concentrate-fed animals (Vasta & Priolo, 2006). Cornu, Kondjoyan, Frencia, and Berdague (2001) discovered several terpenoids, including β -pinene, in beef could be used to determine the region that an animal came from based on volatile compounds from the forages in the geographic area that were ingested by the animal.

Because of sulfur's low threshold, the small amount of these volatile compounds in meat plays a significant role in meat flavor (Drumm & Spanier, 1991) with aldehydes from PUFA playing a role in the synthesis of these heterocyclic compounds (Vasta & Priolo, 2006). Typically, sulfur compounds are in higher concentration in grass-fed cattle because of the tendency of the fatty acids to convert to aldehydes during thermal processing (Elmore, Mottram, Enser, & Wood, 1999).

4.4. Oxidative stability

The source of feed can play a role in the oxidative stability of beef. When cattle were finished on a mixed diet of silage, hay, and concentrate (corn, beet pulp, and linseed cattle-cake), TBARS were always significantly higher than grass-fed animals regardless of age of animal or storage condition of the meat (Gatellier, Mercier, Juin, & Renner, 2005). Brown et al. (1979) also found ground beef from steers on low energy diets had more free fatty acids and lower TBARS than meat from animals that consumed a high energy diet. This was attributed to the increased levels of vitamin E in biological membranes and fat of grass-fed animals although it was noted the grain diet also contained antioxidants of proanthocyanidins and phytic acid (Gatellier et al., 2005). In the same study, a higher heme iron content (considered to be a pro-oxidant) was found in the heifer and cow meat on the mixed diets compared to the grass diets and the steers, which they concluded also affected the increased oxidation. Interestingly, when grain-fed animals are supplemented with vitamin E, the same level of tocopherol is achieved in the lean tissue, and the meat is more stable following 47 d vacuum packaged storage than grass-fed beef with or without supplementation. Therefore, 4–6 $\mu\text{g/g}$ of α -tocopherol in the meat of supplemented grain-fed animals appears adequate to minimize lipid oxidation, but not in grass-fed beef (Yang et al., 2002).

5. Myoglobin and heme iron concentration in beef

It has been suggested myoglobin has a close relationship with lipid oxidation (Renner & Labadie, 1993) which could influence flavor. However, little evidence is present to support these theories even though heme iron, myoglobin, and total iron content have been shown to differ in grass-fed (iron = 3.7 mg/100 g muscle) and grain-fed animals (iron = 2.5–2.7 mg/100 g muscle; Srinivasan, Xiong, Blanchard, & Moody, 1998), different animal maturity levels (older animals have higher levels; Boleman, Miller, Buyck, Cross, & Savell, 1996), and gender (steers have lower levels of heme iron than heifers; Gatellier et al., 2005). Yancey et al. (2006) found livery flavor in beef increased and beef flavor decreased when total iron levels increased in the *M. gluteus medius*. In general, total iron was not a good indicator of beef flavor attributes. This conclusion for total iron was also seen in Jenschke, Eskridge, and Calkins (2006) for normal-flavored beef samples versus liver flavored samples ($P = 0.23$). Small correlations between liver-like flavor and myoglobin concentrations in beef were seen, while hemoglobin relationship to livery flavor was not significant (Yancey et al., 2006).

Heme iron was significantly correlated (-0.51) to off-flavor intensity for just one (*M. vastus lateralis*) of seven muscles from the chuck and round (Meisinger, James, & Calkins, 2006). In this study, regression equations containing linear and quadratic functions of heme iron concentration and muscle pH were established. Some relationships between specific flavors in certain muscles were observed, but with the small number of off-flavored samples no concrete trends were established. However, heme iron has been thought to be a pro-oxidant that may influence meat flavor due to its reaction to produce radicals that can promote lipid oxidation in biological systems (Batifoulier, Mercier, Gatellier, & Renner, 2002; Kanner & Harel, 1985).

6. Effect of pH on flavor

The pH of food plays a role in the development of flavors in the Maillard reaction. As pH increases, color and polymeric compounds increase and nitrogen-containing compounds like pyrazines are favored (Motttram & Madruga, 1994). Since fresh meat only has a pH range of around 5.5–6.0 with a good buffering ability, little work has been done to investigate the effect of pH on Maillard products although meat above the normal pH range is perceived to have a decrease in meat flavor intensity. There has been some thought the higher ultimate pH in meat from grass-fed animals might favor the formation of thiazoles and thiophenones because of the availability of amino acid degradation products while decreasing other sulfur volatiles that favor lower pH (furanthiols, mercaptokin, aliphatic sulfides, and thiopenes: breakdown products of cysteine; Motttram & Madruga, 1994).

Many compounds contributing to beef flavor are water-soluble. As pH increases in meat, the proteins have

increased water binding properties. During cooking fewer water-soluble proteins are lost from high pH meat since there is less cooking loss (Miller, 2001). Dark, firm and dry (DFD) meat is said to have a musty/moldy, covey/grassy, or bloody/serumy aromatic flavors and very high beef flavor intensity (Miller, 2001). High levels of sodium and phosphate in manufactured meats can lead to some of the same flavor perceptions that are in DFD meat. While beef carcasses with lower than average pH are not common, the meat from these animals is usually blander. Lower pH levels can also be attained through the use of acidic ingredients (Miller, 2001).

7. Flavor relationships among muscles

Most of the research comparing muscles has dealt with tenderness because there is approximately 3–4 times the variation between muscles in tenderness compared to flavor (Shackelford, Wheeler, & Koohmaraie, 1995; Wulf & Page, 2000), especially in the *M. longissimus dorsi*. In most studies where flavor or off-flavor scores are determined, the muscle used is the *M. longissimus dorsi*. Over the years some researchers have investigated palatability characteristics, including flavor, from more than one muscle to try to increase the value and usage of specific muscles. Tables 2 and 3 list the rankings of muscles for flavor intensity and off-flavor intensity, respectively, from various studies. In most of the studies the differences in beef flavor intensity between muscles were relatively small.

7.1. Flavor desirability

Beef flavor intensity was positively correlated to off-flavor intensity ($r = 0.71$) and weakly correlated to all other traits (tenderness, $r = -0.14$; amount of connective tissue, $r = -0.11$; juiciness, $r = 0.13$; sarcomere length, $r = -0.31$; percentage of desmin degraded, $r = 0.34$; cooking loss, $r = -0.20$) except collagen concentration and shear force (Rhee, Wheeler, Shackelford, & Koohmaraie, 2004). When simple correlations were run within muscle, every muscle had significant correlations between flavor intensity and off-flavor intensity; the only other correlations with off-flavor intensity were the infraspinatus's correlation to collagen concentration ($r = -0.38$) and the longissimus correlation to juiciness ($r = 0.44$). Jeremiah, Dugan, Aalhus, and Gibson (2003) found no correlations between beef flavor intensity and chemical characteristics for 33 muscles.

Meisinger et al. (2006) found the *M. infraspinatus* had the least off-flavors and the lowest frequency of sour notes of the six chuck and round muscles tested (Table 4). The *M. vastus medialis* had the most intense off-flavor ratings with a high frequency of sour, charred, and oxidized flavor notes. Liver-like, bloody, and rancid flavor notes and heme iron content did not differ among muscles. Off-flavor intensity within the *M. rectus femoris*, *M. teres major*, *M. vastus lateralis*, and *M. vastus medialis* was significantly related to

Table 2
Ranking of muscles^a for flavor intensity from different studies

Rank ^b	1	2	3	4	5	6	7	8	9	10	11
1	LD ^c	IF ^c	DI	BF ^c	TB ^c	CP	LD ^c	LD ^c	SV ^c	SV ^c	LD
2	QF ^{cd}	SV ^c	IF	PM ^{cd}	SM ^c	SP	BF ^d	SM ^c	VI ^{cd}	MD ^{cd}	GM
3	ST ^{de}	CP ^c	BF	GM ^{cd}	LD ^c	TB	SM ^{de}	BF ^c	CP ^{cde}	GR ^{cde}	SM
4	GM ^{def}	LD ^c	SV	SM ^{cde}		SV	TB ^{def}	GM ^c	MD ^{cdef}	PP ^{cde}	
5	SM ^{efg}	PP ^{cd}	IP	TB ^{cdef}		RB	RF ^{efg}		IF ^{cdef}	TB ^{cde}	
6	TB ^{efg}	TB ^{cd}	PM	RF ^{defg}		SL	ST ^{fg}		TB ^{defg}	IF ^{cde}	
7	BF ^{fgh}	SP ^{de}	TM	LD ^{defg}		LT	SP ^{fg}		RB ^{defg}	BF ^{cdef}	
8	SP ^{fgh}	RB ^c	TB	SV ^{defg}		SS	GM ^{fg}		VM ^{defg}	CP ^{cdef}	
9	PM ^{gh}	BB ^e	SP	IF ^{efg}			AD ^g		SS ^{efgh}	VI ^{cdef}	
10	IF ^h		AD	ST ^{efg}			IF ^g		LT ^{efgh}	SL ^{cdefg}	
11			TF	PP ^{fg}			PM ^h		SP ^{efgh}	LT ^{cdefg}	
12			GM	SP ^g					ST ^{efgh}	VL ^{cdefgh}	
13			GR						PP ^{efgh}	SS ^{defgh}	
14			RA						VL ^{efgh}	RB ^{defgh}	
15			PP						SF ^{efgh}	SM ^{defgh}	
16			SD						BF ^{efgh}	SP ^{efgh}	
17			OA						GR ^{fgh}	VM ^{efgh}	
18			SS						RF ^{fgh}	SF ^{efgh}	
19			IC						BT ^{gh}	RF ^{efgh}	
20			VL						SL ^h	AD ^{fgh}	
21			TR						SM ^{hi}	BT ^{gh}	
22			SM						AD ⁱ	ST ^h	
23			RF								
24			LD								
25			ST								

1: Shackelford et al. (1995); 2: Paterson and Parrish (1986); 3: Jeremiah, Dugan, et al., 2003 and Jeremiah, Gibson, et al., 2003; 4: Carmack et al. (1995); 5: Jeremiah et al. (1985); 6: Molina et al. (2005); 7: Rhee et al. (2004); 8: Wheeler et al. (2000); 9: Brickler (2000), dry cookery; 10: Brickler (2000), wet cookery; 11: Wulf and Page (2000).

^a AD = *M. adductor*; BB = *M. biceps brachii*; BF = *M. biceps femoris*; BT = *M. brachiocephalicus*; CP = *M. complexus*; DI = Diaphragm; GM = *M. gluteus medius*; GR = *M. gracilis*; IC = intercostal muscles; IF = *M. infraspinatus*; IP = *M. ilio psoas*; LD = *M. longissimus dorsi*; LT = *M. latissimus dorsi*; MD = *M. multifidus dorsi*; OA = *M. obliquus abdominus internus*; PM = *M. psoas major*; PP = *M. pectoralis profundus*; QF = *M. quadriceps femoris*; RA = *M. rectus abdominis*; RB = *M. rhomboideus*; RF = *M. rectus femoris*; SD = *M. spinalis dorsi*; SF = *M. superficial pectoral*; SL = *M. splenius*; SM = *M. semimembranosus*; SP = *M. supraspinatus*; SS = *M. subscapularis*; ST = *M. semitendinosus*; SV = *M. serratus ventralis*; TB = *M. triceps brachii*; TF = *M. tensor faciae latae*; TM = *M. teres major*; TR = *M. trapezius*; VI = *M. vastus intermedius*; VL = *M. vastus lateralis*; VM = *M. vastus medialis*.

^b Samples are ordered from the most intense beef flavor intensity to the least (bland).

^{c-i} Means within column without common superscript differ.

pH and heme iron, but pH and heme iron were not related to specific off-flavor notes.

Flavor desirability has been used by some researchers in addition to or in lieu of flavor intensity. The Canadian Cattlemen's Association established a goal of 95% consumer acceptance of beef, and seven muscles or muscle groups – *M. teres major*, *M. psoas major*, *M. longissimus thoracis*, *M. longissimus lumborum*, *M. ilio psoas*, *M. spinalis dorsi*, and *M. subscapularis* – fell into that category for flavor desirability (Jeremiah, Gibson, Aalhus, & Dugan, 2003). However, the two longissimus muscles were rated as the second and third lowest for beef flavor intensity, although the range for flavor intensity was fairly small (5.00–6.07 on a 9-point scale) in that study. Five other muscles or muscle groups were approaching 95% desirability for flavor as well.

McKeith, De Vol, Miles, Bechtel, and Carr (1985) found the *M. psoas major*, *M. infraspinatus*, *M. longissimus thoracis*, *M. longissimus lumborum*, and the *M. rectus femoris* to be rated significantly higher than *M. supraspinatus*, *M. semimembranosus*, *M. semitendinosus*, *M. adductor*, and

M. pectoralis profundus for flavor desirability with the *M. biceps femoris*, *M. gluteus medius*, and *M. triceps brachii* being similar to the two groups. Similar findings from Wulf and Page (2000) revealed the *M. longissimus dorsi* and *M. gluteus medius* had the same mean for flavor desirability (5.73 with 8 = intense) while the *M. semimembranosus* was less desirable. Muscle differences in flavor intensity were not due to glycolytic potential, but less than 80 $\mu\text{mol/g}$ affected the *M. longissimus dorsi* for flavor desirability while the *M. gluteus medius* saw a linear increase in flavor desirability with an increase in glycolytic potential (Wulf, Emmett, Leheska, & Moeller, 2002), likely due to ultimate pH. Flavor desirability was highly, negatively correlated ($P < 0.001$) to insoluble collagen in a study that analyzed 33 muscles or muscle groups from 25 Canada AA steer carcasses (Jeremiah, Dugan, et al., 2003).

7.2. Differences in flavor compounds among muscles

In a study using purge and trap mass spectrometry, differences in volatile compounds between raw muscles from

Table 3
Ranking of muscles^a for off-flavor intensity from different studies

Rank ^b	1	2	3	4
1	LD ^c	LD ^c	BT ^c	CP ^c
2	ST ^{cd}	SM ^d	MD ^{cd}	IF ^{cd}
3	GM ^{cd}	TB ^{de}	SS ^{cd}	SL ^{cde}
4	QF ^{de}	BF ^{de}	IF ^{cd}	TB ^{cde}
5	M ^{def}	ST ^{de}	SL ^{cd}	RB ^{cde}
6	BF ^{ef}	RF ^{de}	TB ^{cd}	PP ^{cde}
7	SP ^{ef}	GM ^{de}	VM ^{cde}	MD ^{cde}
8	TB ^{efg}	SP ^{ef}	RF ^{cde}	BT ^{cdef}
9	PM ^{fg}	AD ^{fg}	SV ^{cde}	LT ^{cdef}
10	IF ^g	IF ^g	CP ^{cde}	BF ^{cdef}
11		PM ^g	LT ^{cde}	GR ^{cdef}
12			SP ^{cde}	SV ^{cdef}
13			VL ^{cde}	ST ^{cdef}
14			BF ^{cde}	VL ^{cdef}
15			SF ^{cdef}	SP ^{cdef}
16			VI ^{cdef}	AD ^{cdef}
17			ST ^{cdef}	SM ^{cdef}
18			RB ^{cdef}	SS ^{def}
19			GR ^{cdef}	VI ^{def}
20			SM ^{def}	VM ^{ef}
21			AD ^{ef}	RF ^{ef}
22			PP ^f	SF ^f

1: Shackelford et al. (1995); 2: Rhee et al. (2004); 3: Brickler (2000), dry cookery; 4: Brickler (2000), wet cookery.

^a AD = *M. adductor*; BB = *M. biceps brachii*; BF = *M. biceps femoris*; BT = *M. brachiocephalicus*; CP = *M. complexus*; GM = *M. gluteus medius*; GR = *M. gracilis*; IF = *M. infraspinatus*; LD = *M. longissimus dorsi*; LT = *M. latissimus dorsi*; MD = *M. multifidus dorsi*; PM = *M. psoas major*; PP = *M. pectoralis profundus*; QF = *M. quadriceps femoris*; RB = *M. rhomboideus*; RF = *M. rectus femoris*; SF = *M. superficial pectoral*; SM = *M. semimembranosus*; SL = *M. splenius*; SP = *M. supraspinatus*; SS = *M. subscapularis*; ST = *M. semitendinosus*; SV = *M. serratus ventralis*; TB = *M. triceps brachii*; VI = *M. vastus intermedius*; VL = *M. vastus lateralis*; VM = *M. vastus medialis*.

^b Samples are ordered from the lowest off-flavor score to the highest off-flavor score.

^{c-g} Means within column without common superscript differ.

the chuck and the round were evaluated (Hodgen, Cuppett, & Calkins, 2006). Twenty-eight volatile compounds were identified in all four normal muscles (Table 5). The *M. triceps brachii* did not have any compounds unique from the muscles in the knuckle. The *M. vastus lateralis* had two unique aromatic compounds in its volatile profile. Both of these compounds were in low concentrations relative to other compounds in the sample. The *M. vastus interme-*

dius possessed four compounds that were unique to that muscle, with one of the compounds being unknown. The relative quantity of piperazine and (*Z*)-3-octene in the *M. vastus intermedius* was significantly higher compared to the other compounds that make-up the volatile profile of the muscle. These compounds may help explain why the *M. vastus intermedius* is perceived as having moderately intense flavor (Brickler, 2000; Jones et al., 2004). The *M. rectus femoris* had 10 unique compounds. Additionally, the *M. rectus femoris* had higher concentrations of many of the compounds in comparison to the other three muscles. The beef myology website reports the *M. rectus femoris* has slightly intense flavor whereas the *M. vastus lateralis*, *M. vastus intermedius*, and *M. triceps brachii* have moderately intense flavor (Jones et al., 2004). Apparently, the additional compounds tone down the *M. rectus femoris* flavor so it is not perceived as intense or off-flavored as other muscles in the chuck and round (Brickler, 2000).

Interestingly, mass spectrometry also revealed that the three muscles from the knuckle have 10 additional compounds that are not found in the *M. triceps brachii*. These findings may explain why the *M. triceps brachii* was found to have higher off-flavor ratings than the other three muscles by Brickler (2000).

The different combinations of volatiles may help explain the difference in perceived flavor profile (Hodgen, Cuppett, et al., 2006). The unique compounds of *M. vastus intermedius* create a flavor profile that has higher liver-like, metallic, and rancid characteristics than the *M. triceps brachii*, *M. rectus femoris*, and *M. vastus lateralis* (James & Calkins, 2005). All the volatile compounds in the *M. rectus femoris* may help reduce the sour taste and oxidized, rancid, and charred aromas (James & Calkins, 2005) when compared to the other muscles in this study. While the *M. vastus lateralis* only had two different compounds from the other muscles, the combination of these compounds helped reduce the perceived liver-like characteristic in these samples. Meisinger et al. (2006) found no difference in liver-like between the *M. rectus femoris*, *M. triceps brachii*, and *M. vastus lateralis*.

Cow muscles have very different flavor characteristics compared to meat from A-maturity steer carcasses. A benchmarking study compared sensory properties of muscles from Select, A-maturity carcasses to muscles from four

Table 4
The effect of muscle on percentage of panelists detecting each off-flavor note

Muscle	Liver		Sour		Metallic		Charred		Bloody		Oxidized		Fatty		Rancid	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Infra-spinatus	9.3	2.9	23.2 ^a	3.7	8.7 ^a	2.2	29.9 ^b	4.4	1.6	1.0	9.5 ^{ab}	2.3	14.0 ^b	1.3	8.8	1.6
Rectus femoris	9.7	2.9	44.2 ^b	3.7	13.4 ^a	2.2	20.4 ^{ab}	4.4	3.4	1.0	7.4 ^a	2.3	3.2 ^a	1.3	4.9	1.6
Teres major	8.8	2.9	48.7 ^b	3.7	15.5 ^{ab}	2.2	21.6 ^{ab}	4.4	1.8	1.0	8.5 ^{ab}	2.3	3.3 ^a	1.3	5.8	1.6
Triceps brachii	7.7	2.9	49.5 ^b	3.7	19.5 ^b	2.2	22.2 ^{ab}	4.4	0.8	1.0	13.3 ^{abc}	2.3	1.6 ^a	1.3	5.6	1.6
Vastus lateralis	9.1	2.9	48.4 ^b	3.7	15.0 ^{ab}	2.2	30.5 ^b	4.4	1.3	1.0	17.5 ^c	2.3	1.4 ^a	1.3	6.8	1.6
Vastus medialis	10.8	3.0	49.0 ^b	3.8	17.3 ^{ab}	2.2	14.8 ^a	4.6	2.9	1.0	14.6 ^{bc}	2.3	2.3 ^a	1.4	7.2	1.6

Taken from Meisinger et al. (2006).

^{a,b,c} Means within a column (for off-flavor notes) with different superscripts are significantly ($P < 0.05$) different.

Table 5

Compound concentration differences for between normal-flavored beef muscles^a determined by gas chromatography–mass spectrometry analysis

Retention time ^b	Compound ^{c,d}	TRI	REC	VAL	VAI
1.93	UNK	×		×	×
2.03	UNK		×	×	×
2.48	Oxirane, 2,3-dimethyl-	×	×	×	↑
2.81	UNK				×
3.07	1,2-Ethanediamine, <i>N,N'</i> -dimethyl	×	×		
3.09	Pentanal			×	×
3.12	<i>sec</i> -Butanamine		×		
3.15	UNK		×		
3.17	Cyclobutanol	×			
3.20	UNK		×		×
3.45	2-Heptanamine, 5-methyl	×			
3.50	UNK		×		×
3.65	Pentanal	×			
3.71	Pentanal	↑	×	×	×
4.41	Piperazine				×
4.77	Cyclobutanol		×		×
4.88	UNK		×		×
5.29	1-Pentanol	×	↑	×	×
5.56	1-Pentanol, 5-amino		×		
5.82	UNK		×	×	
5.86	UNK		×		×
6.11	Hexanal	×	↑	↓	×
6.27	3-Octene, (<i>Z</i>)-				×
6.44	1,3-Propanediamine, <i>N</i> -methyl or hexanal		×		
6.49	2-Heptanamine, 5-methyl		×		×
7.60	UNK		×		×
8.05	1-Hexanol	↑	↓	↑	↓
8.18	UNK				×
8.25	1-Hexanol			×	
8.62	2-Heptanone	×	×	×	×
8.88	Heptanal	↓	↑	×	×
9.72	α -Pinene	×	×	×	×
10.32	2-Heptenal	×	↑	×	×
10.43	Benzaldehyde	×	×	×	×
10.60	2-Hexen-1-ol, (<i>E</i>)-		×		
10.67	1-Heptanol	↓	↑	×	↓
10.83	β -Pinene	×	×		×
10.90	1-Octen-3-ol	×	×	×	↓
11.01	<i>n</i> -Capric acid vinyl ester or 3-octanone, 2-methyl	×	↑	×	×
11.19	Furan, 2-pentyl	↓	×	↑	↓
11.47	Octanal	↓	↑	×	↓
11.66	3-Carene		×		×
12.10	1-Hexanol, 2-ethyl-	×	×	×	×
12.20	1,3-Hexadiene, 3-ethyl-2-methyl-		×		×
12.35	3-Octen-2-one		×		
12.49	UNK	×	×	×	×
12.77	2-Octenal, (<i>E</i>)-	×	↑	×	×
13.00	2-Octen-1-ol or 1,3-octadiene	×	×	×	×
13.05	1-Octanol	↓	↑	×	↓
13.41	UNK		×		×
13.52	2-Nonanone			×	
13.63	Octadecanal		×		
13.80	Nonanal	↓	↑	×	×
14.28	UNK		×		
14.83	3-Hydroxymandelic acid, ethyl ester, di-TMS or benzaldehyde, 2,4-bis(trimethylsiloxy)-	×	×	×	×
14.99	2-Nonenal or 1-tetradecene	×	↑	×	×
15.13	UNK		×	×	
15.69	Undec-4-enal		×		
15.92	Decanal	×	×	×	×
16.11	2,4-Nonadienal		×		
16.93	Benzene, 1,3-bis(1,1-dimethylethyl)-				×
17.03	2-Decenal	×	↑	×	×
17.39	UNK		×	×	

(continued on next page)

Table 5 (continued)

Retention time ^b	Compound ^{c,d}	TRI	REC	VAL	VAI
17.66	2,4-Decadienal		×	×	
17.71	Tridecane	×	×	×	×
18.09	2,4-Decadienal		×	×	×
18.19	Malonic acid, bis(2-trimethylsilylethyl ester)	↓	↑	×	↑
18.93	2-Tridecenal		×	×	×
19.51	Tetradecane		×	×	
19.71	Oxirane, hexadecyl or UNK	×	×	×	×
21.20	UNK		×	×	×
21.43	UNK	×	×	×	

Taken from Hodgen (2006).

^a TRI = *M. triceps brachii*, REC = *M. rectus femoris*, VAL = *M. vastus lateralis*, and VAI = *M. vastus intermedius*.

^b Retention time was obtained from GC–MS report for each sample.

^c Compounds listed were matches found in the mass spectrometry database.

^d ↑ indicates that a higher concentration of the compound was found in that type of sample; ↓ indicates that a lower concentration of the compound was found in that type of sample; × indicates the compound was present and/or fell in between higher and lower than ones listed with an arrow.

cow populations (beef-fed, beef-nonfed, dairy-fed, dairy-nonfed) (Stelzleni, Johnson, Calkins, Mink, & Gwartney, 2005). All muscles from cows had more intense beef flavor and greater off-flavor than muscles from younger, A-maturity Select-grade beef carcasses.

In a study conducted in our laboratory (Meisinger et al., 2006), seven muscles from the chuck and knuckle were obtained from 30 animals, and animal identity was maintained. Three animals had the majority of their muscles ranked 5 or below on an 8 point hedonic scale for off-flavor intensity (Table 6) which meant the off-flavor was approaching or below what average consumers would find acceptable. These data suggest that when an animal has one muscle in the chuck or knuckle that has off-flavor, other muscles in the chuck or knuckle are likely to be off-flavored as well. This suggests there is an ‘animal effect’ to off-flavors found in the chuck and knuckle, meaning the animal has been exposed to something different than a normal animal. After investigating several angles, our laboratory’s current hypothesis is the difference is caused at least partially by the diet of the animal.

This ‘animal effect’ on flavor leads to other questions that need to be addressed. Do all muscles in a candidate animal for off-flavor possess off-flavor? Is it just locomotion muscles or muscles that lay on or near a bone? Most importantly, what is causing these undesirable flavors and how can producers, processors, or individuals preparing the meals mitigate or eliminate the effect?

8. Liver-like off-flavor in beef

With the increased use of muscles from the chuck and round in the US for steak items, rather than roasts or ground beef, restaurant personnel and foodservice employees that use these steaks have reported an increased number of complaints regarding the flavor of the beef they serve. The majority of the complaints are referred to as liver-like flavor. Because of the economic impact these steaks have on the beef industry, it is important to identify and understand the causes of this particular off-flavor.

8.1. Cooking rate and holding time

Most of the anecdotal reports of incidences of off-flavors our laboratory received were from foodservice personnel. It was hypothesized that since foodservice preparation traditionally cooked the meat quickly and then held the product in warming ovens until the food was presented to the consumer these conditions might promote the liver-like flavor. Seven muscles located in the chuck and knuckle were slowly or rapidly cooked (on a 149EC commercial gas grill or a 249EC grill) and held for 0 or 1 h prior to consumption. Results clearly demonstrated that cooking at a slower rate and holding for a longer time reduce the intensity of off-flavor. It is hypothesized the slower cooking and longer hold time allow the undesirable volatile compounds to dissipate (James & Calkins, 2005).

Table 6
Mean off-flavor intensity scores and the percentage of panelist’s who recognized liver-like flavors

Animal	Off-flavor intensity scores						Percentage of panelist’s who recognized liver-like flavor -					
	Infra-spinatus	Rectus femoris	Teres major	Triceps brachii	Vastus lateralis	Vastus medialis	Infra-spinatus	Rectus femoris	Teres major	Triceps brachii	Vastus lateralis	Vastus medialis
6	3.78	3.78	1.60	2.22	3.00	2.30	66.70	44.40	30.00	44.40	62.50	60.00
7	4.88	3.38	2.67	4.00	3.57	4.60	12.50	50.00	66.70	11.10	42.90	60.00
8	3.88	4.88	4.90	4.50	3.57	3.90	100.00	50.00	50.00	37.50	37.50	60.00

Adapted from Meisinger et al. (2006).

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During this study the observation was made that the samples that would be rated as having intense off-flavor by the trained taste panelists could be smelled during the cooking process. With the knowledge that there appears to be an animal effect and that the off-flavor is at least somewhat volatile, our laboratory has taken two directions in determining the cause of this off-flavor – pre-harvest conditions and compounds differences between lean tissue that is normal and lean tissue that is liver-like in flavor.

8.2. Frequency

The frequency of this off-flavor appears to relatively low, although the initial speculation was the incidence was between 7% and 10% based on Yancey et al. (2006) and Meisinger et al. (2006). In a survey of urban Nebraska residents, 6.9% (11 out of 159) of respondents who had eaten a *M. infraspinatus* steak stated they had a poor eating experience due to flavor.

8.3. Sniff test

To develop a sampling method for off-flavored beef samples, 10 g slices of the knuckle were sliced off on the fabrication line in a packing plant, cooked immediately in a room with air purifiers and smelled and/or tasted to determine if the sample was off-flavored. Samples that were thought to be off-flavored by this test were taken to the meat laboratory at the University of Nebraska and reevaluated by the panelists that had performed the evaluation at the plant. Contingency tables revealed the panelists were in close agreement, but there were few samples with the liver flavor (Jenschke, Hamling, et al., 2006). Further work is needed to confirm the usefulness of this method to study liver-like off-flavors.

8.4. Feedlots and pre-harvest conditions

A total of 328 knuckles, which came from five different feedlots, were tested by the two panelists. Utilizing smelling and tasting, feedlot A had 5.0% off-flavored samples (1 of 20), feedlot B had 9.4% (5 of 53), feedlot C had 6.7% (10 of 148), feedlot D had 12.5% (9 of 72) and feedlot E had 14.3% (5 of 35) (Jenschke, Hamling, et al., 2006).

No relationships between any of the pre-harvest traits or liver scores and the prevalence of off-flavors existed. There were also no trends in muscles having liver-like flavor and medical treatment or feed additives received (data not shown). Since distribution of off-flavors varied among feedlots, future research should investigate pre-harvest factors that might lead to off-flavor development.

8.5. Minerals and fatty acids

The liver-like flavor in beef is often associated with an increase in metallic flavor (Miller, 2001) and increased

cooler aging (Campo, Sanudo, Panea, & Alberti, 1999). Our laboratory investigated the relationship of eight minerals and fatty acids to the liver-like off-flavor. Sodium, 16:1, 18:1n7 (vaccenic acid), 20:2n6, and 20:3 accounted for 46% of the variation between liver-like samples and controls. Sodium relationship was low in this study, but we hypothesize sodium may help accentuate the liver-like off-flavor and that is why it fell into the model. Iron has often been thought to play a role in the liver-like off-flavor (Yancey et al., 2006) but this mineral did not show up in any of our analyses. Our fatty acid analysis revealed similar results to others (Camfield et al., 1997; Yancey et al., 2006) with medium and long chain unsaturated fatty acids playing a role in creating the liver-like off-flavor. Regression models of unsaturated fatty acids alone accounted for 40% of the variation in liver-like off-flavor. Further understanding of manipulation of unsaturated fatty acids in muscle tissue could prove beneficial in reducing the incidence of the liver-like off-flavor. Current research is being undertaken to consider a more complete picture of the fatty acid profiles between off-flavored and normal samples. Sulfur level comparisons between the liver-like and the normal samples need to be determined since this mineral could create undesirable flavors.

8.6. Gas chromatography–mass spectrometry

With the evidence the liver-like off-flavor is partially due to a volatile compound, gas chromatography and mass spectrometry work was conducted to evaluate the differences between compounds in liver-like beef samples and normal-flavored samples. Raw meat samples (5 g) were mixed with 100 mL of double distilled water in a closed container with an inlet to push nitrogen through and an outlet to smell aromas emitted from the sample when heated in a 40 °C water bath (Table 8; Hodgen, Calkins, & Cuppett, 2006). Undesirable aromas were emitted only for the samples that were ranked by taste panelists as being liver-like while normal beef aromas were emitted from the control samples. When these compounds were collected and injected into the gas chromatograph, differences in chromatograms were observed between the normal and liver-like samples.

The raw, pulverized samples were run on a purge and trap mass spectrometer (Hodgen, Cuppett, et al., 2006). Because muscle tissue heated only to 40 °C showed differences in volatile composition between normal and liver-like samples, it was decided to eliminate much of the effect of the cooking process by using raw tissue samples to reduce the amount of compounds produced. This would reduce the number of compounds produced by the Maillard reaction, but compounds that help give rise to the liver-like flavor would still be present. Differences in the presence of numerous compounds were apparent between normal and liver-like samples. Most of the compounds present in higher concentration in the liver-like samples, like penta-

nol, hexanal, hexanol, 1-octen-3-ol, and nonanal, are associated with lipid oxidation (Table 7). The compounds β -pinene, 1-octen-3-ol, and 2,4-decadienal were in higher concentration in the liver-like samples in all muscles tested. Several of these same compounds were implicated by Yancey et al. (2006) when they used cooked samples for evaluation between liver-like and normal samples. Interestingly, these compounds (especially 2,4-decadienal) are associated with the offensive odor of *Eocanthecona furcellata* (Wolff) – commonly known as the stink bug (Ho, Kou, & Tseng, 2003). Limonene, a citrus aroma, was observed in higher concentrations in the liver-like samples in their study and in later studies in our laboratory (Hodgen, 2006). In the original study (Hodgen, Cuppett, et al., 2006), the compound with the same retention time as limonene was identified by the mass spectrometer database as a hexanol isomer so it is likely this compound also contributes to the liver-like aromatic profile in samples.

A larger pool of samples are needed to further investigate the volatile make-up of liver-like samples. Further investigation into oxidation also needs to be addressed in regards to liver-like flavor. Both Hodgen, Cuppett, et al. (2006) and Yancey et al. (2006) found compounds associated with lipid oxidation, yet thiobarbituric acid assays found no relationship (Yancey et al., 2006) between normal and liver-like samples.

8.7. A candidate cause

While the liver-like off-flavor has been around for many years, there is speculation the increase in incidence of liver-like samples may be attributed to changes in feeding practices in the US. Some evidence points to increased levels of unsaturated fatty acids in the muscle in liver-like samples, so feedstuffs that have higher levels of unsaturation have been suspect. The biohydrogenation process in ruminant animals minimizes passage of unsaturated fatty acids through the digestive system. One possible candidate out laboratory has investigated is wet distillers grain plus solubles (WDGS) since the increased use of distillers grain seemed to coincide with the increased complaints about liver-like flavor in meat. Feedlots receiving this by-product of ethanol production also have to ensure sulfur levels in the animal feed will not reach undesirable levels as the ethanol processing method uses sulfur. Sensory results in meat from a feeding trial in which steers were fed 0%, 10%, 20%, 30%, 40%, and 50% levels of WDGS did not show any significant relationship ($P = 0.07$) to the perception of liver-like off-flavor in the *M. rectus femoris* although it was approaching significance (Table 8; Jenschke, Hodgen, Vander Pol, Calkins, & Klopfenstein, 2006). However, this work was conducted on meat aged 7 d. Storage (aging) of meat would allow oxidation to occur.

Table 7

Compound concentration differences between the liver-like and normal-flavored beef muscles determined by gas chromatography–mass spectrometry analysis

Compound ^{a,b}	TRI ^c		REC ^c		VAL ^c		VAI ^c	
	Liver-like	Normal	Liver-like	Normal	Liver-like	Normal	Liver-like	Normal
2,3-Dimethyl oxirane							↑	↓
Pentanal	↑	↓					↑	↓
Heptanol	↑	↓						
Hexanal	↑	↓						
Hexanol								
2-Heptanone	↑	↓						
Heptanal	↑	↓						
Benzaldehyde	↑	↓						
β -Pinene	↑	↓	↑	↓	↑	NP	↑	↓
1-Octen-3-ol	↑	↓	↑	↓	↑	↓	↑	↓
2-Methyl-3-octanone or <i>n</i> -caproic acid, vinyl ester	↑	↓			↑	↓	↑	↓
2-Pentyl furan	↑	↓					↑	↓
Octanal	↑	↓					↑	↓
α -Pinene	↑	↓					↑	↓
2-Octenal	↑	↓					↑	↓
1-Octanol	↑	↓					↑	↓
Nonanal	↑	↓			↑	↓	↑	↓
Hydroxymandelic acid							↑	↓
2-Nonenal							↑	↓
1,3-Bis(1,1-dimethylethyl) benzene	↑	NP	↑	↓	↑	↓	↑	↓
2,4-Decadienal	↑	NP	↑	↓	↑	↓	↑	↓
2,4-Decadienal	↑	NP	↑	↓	↑	↓	↑	↓

Taken from Hodgen (2006).

^a Compounds listed revealed visual concentration differences in chromatograms.

^b ↑ indicates that a higher concentration of the compound was found in that type of sample; ↓ indicates that a lower concentration of the compound was found in that type of sample; NP = not present.

^c TRI = *M. triceps brachii*, REC = *M. rectus femoris*, VAL = *M. vastus lateralis*, and VAI = *M. vastus intermedius*.

Table 8

Least squares means for main effects for off-flavor intensity, liver-like and metallic off-flavors

Effect	Off-flavor intensity ^a	Liver-like ^b	Metallic ^b
Treatment ^c	0.47 ^d	0.07 ^d	0.73 ^d
0	5.72	14.44	34.07
10	5.49	19.63	27.41
20	5.69	11.85	31.85
30	5.74	7.41	31.85
40	5.54	12.22	34.81
50	5.73	8.52	36.30
Standard error of the mean	0.11	3.07	4.17
Quality grade	0.002 ^d	0.03 ^d	<0.001 ^d
Choice	5.51 ^e	15.19 ^f	39.26 ^f
Select	5.80 ^f	9.51 ^e	26.17 ^e
Standard error of the mean	0.07	1.77	2.41

Adapted from Jenschke, Hodgen, et al. (2006).

^a Off-flavor intensity: 1 = extreme off-flavor; 8 = no off-flavor.^b Off-flavors are expressed as a percentage of panelists that identified the off-flavor.^c Treatments: percentage of wet distillers grains plus solubles included in diet.^d P-value from analysis of variance tables.^{e,f} Mean values within a column and followed by the same letter are not significantly different ($P > 0.05$).

Further research has been conducted in our laboratory to investigate the relationship of flavor to meat properties from steers fed WDGS. Increases in polyunsaturated fatty acids were seen with an increase in WDGS levels in the diet (4.90% of fatty acid methyl esters versus 5.91% and 6.23% of fatty acid methyl esters for cattle fed 15% or 30% WDGS on a dry matter basis). Our results (unpublished) also show an increase in oxidation and a decrease in color stability when WDGS are fed. Similarly, Roeber, Gill, and DiCostanzo (2005) found some reduction in color stability upon storage for beef from cattle fed distillers grains.

Approaching the cause of liver-like off-flavors in beef chuck and round muscles from a pre- and post-harvest view has increased our knowledge about the liver-like flavor, but further research is still needed to be able to prevent the occurrence of this undesirable flavor from occurring.

9. Conclusions

Development of the flavor of meat is a very complex system. Factors that make some meat desirable and other meat undesirable is influenced by many conditions, including pre-harvest animal environment and diet, post-harvest handling, and consumers' individual preferences. The first two factors can be investigated and solutions can be determined; the latter is a much harder variable to control since a person's internal and external influences help develop personal preferences. The role of the meat industry should be to try to produce the highest quality product for the market they are targeting.

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