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Sheepmeat Flavor and the Effect of Different Feeding Systems: A Review

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ABSTRACT: Lamb has a unique flavor, distinct from other popular red meats. Although flavor underpins lamb's popularity, it can also be an impediment to consumer acceptance. Lack of familiarity with sheepmeat flavor itself can be a barrier for some consumers, and undesirable feed-induced flavors may also compromise acceptability. Against the backdrop of climate uncertainty and unpredictable rainfall patterns, sheep producers are turning to alternatives to traditional grazing pasture systems. Historically, pasture has been the predominant feed system for lamb production in Australia and around the world. It is for this reason that there has been a focus on "pastoral" flavor in sheep meat. Pasture-associated flavors may be accepted as "normal" by consumers accustomed to meat from pasture-fed sheep; however, these flavors may be unfamiliar to consumers of meat produced from grain-fed and other feed systems. Over the past few decades, studies examining the impacts of different feeds on lamb meat quality have yielded variable consumer responses ranging from "no effect" to "unacceptable", illustrating the diverse and sometimes inconsistent impacts of different forages on sheepmeat flavor. Despite considerable research, there is no consensus on which volatiles are essential for desirable lamb aroma and how they differ compared to other red meats, for example, beef. In contrast, comparatively little work has focused specifically on the nonvolatile taste components of lamb flavor. Diet also affects the amount of intramuscular fat and its fatty acid composition in the meat, which has a direct effect on meat juiciness and texture as well as flavor, and its release during eating. The effect of diet is far from simple and much still needs to be learned. An integrated approach that encompasses all input variables is required to better understand the impact of the feed and related systems on sheepmeat flavor. This review brings together recent research findings and proposes some novel approaches to gain insights into the relationship between animal diet, genetics, and sheepmeat quality.

KEYWORDS: *sheepmeat flavor, lamb, aroma, taste, olfactometry, diet, feed*

INTRODUCTION

An estimated world total population of about 1 billion sheep[1] exists for wool, milk, and meat production. The largest number are in China, about 130 million, followed by Australia (70 million), India (65 million), Iran and Sudan (50 million each), and Nigeria, New Zealand, and the United Kingdom (30 million each). Most of the sheep produced in China are destined for local consumption, whereas Australia and New Zealand, by contrast, are major sheepmeat exporters despite high local consumption, particularly in New Zealand. In these countries, the production systems vary, ranging from pasture to grain feeding.[2] In Australia, the majority of lamb production is based on pasture as a feedstock with some grain supplementation; however, although it represents only a minor share of the market, there has been a recent trend for finishing lambs with grain-based rations in a confined feeding system.[3] The feeding regimen used for lamb production is important because it directly affects sheepmeat quality.[4]

Meat quality is defined by those traits that the consumer regards as important to acceptability, which include both visual and sensory traits, credence traits of safety and health, and those that relate to the ethical nature of the production system.[5] Important visual traits include the color and texture of the meat, fat color, and amount and distribution of fat, as well as the absence of excess water (purge) in the retail tray.[6] Once cooked, consumer satisfaction is largely determined by how tender the meat is and its flavor and juiciness.[6] Consumers of sheepmeat usually place the highest weighting on flavor, followed by tenderness and last juiciness.[7,8] This is in contrast to beef meat, for which the highest weighting is placed on tenderness.[9]

Flavor refers to the components of food responsible for chemosensory stimulation: volatile aroma and nonvolatile taste compounds. Flavor molecules must interact with sensory receptors to be perceived; flavor information is normally integrated together with texture, visual, and other sensory cues by the brain to create a unique sensory signature. The type, quantity, and balance of flavor molecules are critical to the acceptability of meat flavor, and the structure and composition of the meat affects the way that flavor molecules are released during cooking and eating. Additionally, flavor perception is influenced by the extent to which potentially flavorful compounds are released and made available to receptors. The composition of the meat, particularly the fat content (acting as a solvent for flavor compounds) and structure (e.g., density of myofibrillar proteins) will also affect the release of flavor compounds. In this respect, it is the preparation and cooking of

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meat that also have a large effect on the overall flavor and eating quality.

In its fresh uncooked state, meat has little flavor; it is only as a result of cooking that full flavor develops. During cooking, a complex set of thermally induced reactions occur between the nonvolatile components of lean and fat tissue, which results in the generation of a large number of products. The final array of flavor compounds collectively forms the species-specific flavor for that animal.[10] The major precursors of meat flavor are either lipids or water-soluble components, which are subject to two sets of reactions during the cooking process: Maillard reactions between amino acids and reducing sugars, and oxidative degradation of the lipid components. Principally, the lipid-derived volatile compounds are responsible for explaining the differences between volatile profiles of meat species and, thus, are the compounds that contribute to the species-specific flavor.

Historically, the focus of attention for sheepmeat flavor has been given to the aroma of cooked meat particularly in relation to 'mutton' and 'pastoral' flavors. 'Mutton' flavor is related to the age of the animal and is more commonly associated with the cooked meat taken from older animals, whereas 'pastoral' flavor is related to pasture diet fed to the animal.[8] These, however, are not the only characteristic "flavor notes" that have been reported to be present in sheepmeat. For example, brassica as a feedstock has been found to impart a taint to cooked sheepmeat regarded as unacceptable by consumers[11,12] and, although less common, microbial spoilage can also introduce a 'potato' aroma to uncooked sheepmeat.[13] Previous reviews have been published that relate diet to sheepmeat flavor.[14,15] The purpose of this paper is to provide an integrated overview of the impact of feeding systems (as pasture or grain and/or supplementation) on sheepmeat flavor, how this may vary with genetics, and also to define the consumer response to sheepmeat. A brief description of forage composition and sheep digestion of nutrients is given to explain the possible contribution to sheepmeat flavor.

■ FORAGE COMPOSITION AND ITS POSSIBLE INFLUENCE ON FLAVOR

Sheep that are growing and depositing muscle and fat have nutrient requirements which need to be met by the available feed. The main requirement is for energy, and the energy value of a feed is expressed as megajoules of metabolizable energy (ME) per kilogram as dry matter.[16] The nutritive value of a pasture can generally be described by the ME and crude protein (CP) content, which measures the quality, and the "feed on offer" (FOO), which indicates the quantity. When combined, FOO with the ME and CP content are used to estimate the growth rate (see ref 17, for example). In addition to these basic measurements, water-soluble carbohydrate (WSC) and neutral detergent fiber (NDF) can also be used to more precisely determine the nutrient availability from pasture.[18]

The supply to meet the protein requirements of a growing sheep is dominated by that flowing from the rumen to the small intestine.[19] For lambs growing at the recommended growth rate of 0.2 kg day^{-1},[20] the recommended ME and protein intakes are 12.5 MJ day^{-1} and 13% (as crude), respectively.[16] Inevitably, variability will exist in the content of these different nutrients for pasture[18,20] and, at times of low digestibility, hay and/or grain will be used as a feed supplement for sheep. Additionally, when the protein content is limiting in feeds such as tropical or subtropical pastures during the dry season or Mediterranean-type pastures during summer, the feed can be supplemented with additional protein or alternatively a non-protein-nitrogen (NPN) source to makeup for this deficiency.

Pasture species vary in their content of carbohydrates,[21,22] glucosinolates,[23] and crude protein as well as their digestibility[24−27] between seasons, years, and fertilizer applications as well as between pasture variety and species. For example, in the case of subterranean clover (*Trifolium subterranean*), crude protein content can vary from 17 to 30%, whereas, for perennial ryegrass (*Lolium perenne*), the protein content can range from 5 to 19% between seasons and also years.[25] Another example is in New Zealand, where higher total nitrogen concentrations have been found in local pasture over the cooler months compared to that grown in the summer period,[28] with variability in dry matter, NDF, acid detergent fiber, and soluble carbohydrate also being evident.[24] This variation in pasture composition will affect the animal's deposition of muscle, fat, and glycogen, but it also affects the absorption of nutrients. It is evident that such variations in pasture composition are likely to affect the deposition of compounds that contribute to flavor in the muscle tissue, as described in the following sections. It also becomes apparent that, as animal production systems become more sophisticated with greater emphasis on meeting consumer demands with better end-product quality, describing pasture quality by ME and CP content alone will most likely become obsolete and other means for description will be needed.

Prior to slaughter, forages can influence muscle development, carcass fatness, and intramuscular fat (IMF) content through the levels of ME and CP and an interaction with the genetic propensity of the animal for muscle and fat deposition. The IMF content present in the muscles of a sheep carcass can have an positive influence on the overall liking and flavor scores given by a consumer panel.[29,30] IMF is late in developing because other fat depots, such as subcutaneous and mesenteric depots, develop earlier.[31] In lambs finished for meat production, IMF levels generally range from 1 to 9%,[32] and fat levels below 3−5% are thought to negatively afffect consumer acceptability,[30,33] relative to higher IMF levels.

The fatty acid composition of pasture is predominately α-linolenic acid, the parent molecule of the n-3 polyunsaturated fatty acid (PUFA) family,[34] which is highly regarded due to its overall positive contribution to health and nutrition.[35] Long-chain (LC) PUFAs can be synthesized from α-linolenic acid during the process of fat metabolism in sheep.[34] Compared to grain concentrate, using pasture as a feedstock for sheep has been shown to increase the PUFA content of the associated meat.[36] In comparison, the major fatty acid found in grains is linoleic acid,[37] the parent molecule for the n-6 PUFA family. The latter group of PUFAs are not favorably regarded, though, because they counteract the positive contribution made from the n-3 LC PUFAs when the dietary ratio of n-6:n-3 is high.[34] Both n-3 and n-6 PUFAs are important contributors to the odor of lamb fed pasture and grain, respectively, with acceptance of the final cooked meat product being influenced by the preference of the consumers and their familiarity with the product.[35]

Species of brassicas, such as forage rape and kale, have been increasingly used in Mediterranean climates as a good source of nutrition for livestock during autumn and winter. Varieties of brassicas are known to contain compounds called glucosinolates, which are considered to impart an offensive odor to the meat of lambs grazing such plants preslaughter.[11] When used, it is recommended that lambs are withdrawn from any brassica forage or canola stubble from 3 to 7 days prior to slaughter;[38,39]

Table 1. Impact of Various Feeding Regimens on Flavor of Sheepmeat

feeding system	impact on flavor	attribute[a]	ref
	Untrained Panel		
chicory vs lucerne	no difference	F	12
rape vs pasture	stronger, less acceptable flavor for rape	F	12
white clover, lucerne, lotus, ryegrass vs corn, corn + fescue	corn finished samples more than forage finished	F + O	41
pasture vs concentrate vs pasture/concentrate	differences based on consumer (country) preference	F	190
saltbush vs barley/lupin/hay	no difference	F	55
mixed pasture vs grain-based or poor quality dry feed	no difference between pasture vs grain	F	46
milk vs milk replacer (rearing system)	no discrimination	F	139
	Trained Panel		
white clover vs ryegrass	stronger flavor/odor for white clover	F + O	49
lucerne vs perennial ryegrass	more intense flavor/odor for lucerne	F + O	50
ryegrass, tall fescue, cocksfoot, phalaris, lucerne, chicory, prairie grass	phalaris ("foreign flavor") stronger than others	F + O	123
lucerne vs phalaris	lucerne less acceptable than phalaris	F	186
lucerne	lucerne related flavor increased	F	187
lotus vs ryegrass vs white clover	no influence on meat flavor; (*p*-cresol negatively correlated with sheepy odor)	F	56
cultivated pasture vs mountain pasture	minor differences in 'metallic' and 'rancid'	F + O	26
Brassica rapus vs pasture	*Brassica*, strong, unattractive odor/flavor	F	11
rape, vetch, oats vs pasture	low acceptability for rape	F	51
	some differences found for vetch and oats		
tropical legumes vs grass	no significant difference	F	52
grass/clover vs chicory	no appreciable difference	F + O	54
alfalfa vs corn/soybean	flavor more intense for alfalfa	F	39
parthenium weed vs grain	panel could differentiate "taint", differences small	F	40
pasture vs concentrate vs pasture/concentrate	lower acceptance of pasture-fed animals	F	191
cottonseed meal vs corn dried distillers grains	no difference	F + O	192
perennial ryegrass + other grasses vs grain-based	"sheepmeat" higher for pasture than grain	F + O	42
pasture vs grain concentrate	"lamb" flavor higher in concentrate. grass-fed animals; higher in "liver" flavor	F + O	188
pasture vs lucerne or maize concentrate	"sheepmeat" higher for pasture	F + O	44
ryegrass vs concentrate	"off" odors/flavors in pasture-fed meat	F	105
ryegrass vs saltmarsh, heather, moorland	ryegrass less acceptable than others		189

[a]Flavor attribute tested: F, taste; O, odor/aroma.

however, anecdotal evidence suggests that 2 weeks may be required. There is a large variation between, and within, different varieties of brassicas in their content of glucosinolates, even when grown under similar conditions.[23] For example, under controlled and similar environments, the forage rapes *Brassica napus* and *B. napus oleifera* contain, respectively, 3−15 and 21−35 μmol g^{-1} of total glucosinolates.[23] Further discussion on brassicas and sheepmeat flavor is given in the next section.

EFFECT OF FEED SYSTEMS ON COOKED SHEEPMEAT FLAVOR AS ASSESSED BY SENSORY PANELS

The use of a pasture-based finishing diet for sheep, compared to a grain-based one, can significantly affect the sensory properties of the cooked meat (Table 1). Pasture, in comparison to grain, introduces a different flavor to the final product, which is perceptible by trained sensory panels.[36−45] Some authors have assigned the flavor resulting from pasture feeding to the species-specific flavor associated with cooked sheepmeat (e.g., "*sheepmeat*",[42,46] "*lamb*"[47]). The presence of a pasture-based flavor is regarded as a taint by some consumers.[48] However, this may be more related to consumer habituation because that study was performed in the United States where consumers are more accustomed to meat from grain-fed animals compared to that from grass-fed animals.

Within pasture types, differences in sheepmeat flavor have been reported because of the feed material. For example, in comparative trials of different pasture species, unacceptable flavors have been found by trained panels for white clover,[49] lucerne and phalaris,[47,49,50] and rape (*Brassica*);[11,12,51] a more complete list is shown in Table 1. In contrast, other studies have not been able to find any sensory differences associated with the meat of animals fed different forage species.[52−56] Of course, this also highlights the differences that exist within these panels, ranging from no apparent difference to those that are unacceptable to consumers. These differences may be related to the use of similar terms that are used differently by various panels and so lead to conflicting conclusions within the literature. In such cases, it would have been useful to have a common lexicon shared by the different groups to assess the cooked meat samples.

In some instances, the impact of the pasture species on sheepmeat flavor can be quite significant. As noted above, forage rape (*Brassica*) has increasingly been used as a feed source for sheep. There have been reports, though, that the resulting flavor in the final cooked meat product has been regarded as "strong and unattractive" by a trained sensory panel[11] and as "unacceptable" by an untrained consumer panel.[12] In these cases, the volatile compounds responsible for these aromas would most likely have been present in sufficient concentration to be detected by gas chromatography−mass spectrometry (GC-MS). Because GC-MS was not used, it is not

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possible to identify the compounds responsible for the disagreeable flavor. However, in the case of forage rape, there are reports in the literature that can be used to present a plausible mechanism for the presence of this "unacceptable" flavor in the cooked meat from brassica-fed animals. In Australia, cultivars of rapeseed (*Brassica*) are known to contain glucosinolates in concentrations >30 μmol g^{-1} (dry weight).[57] Once consumed, the metabolites from the glucosinolates are absorbed and can then be transported by the blood supply for deposition into either muscle or fat and thus are potential contributors to meat flavor. Additionally, these compounds can be metabolized by the animal to form products such as isothiocyanates, nitriles, and thiocyanates.[58] Isothiocyanates are volatile compounds and are known to be extremely pungent (for example, in wasabi[59]) and so could significantly contribute to the flavor of the final cooked product. We speculate that on the basis of reports in the literature glucosinolates are metabolized by sheep to produce isothiocyanates. High levels of serum isothiocyanate have been found in the blood of sheep that have been fed high-glucosinolate mustard (*Brassica juncea*) meal.[60] These authors attribute these levels directly to the consumption of glucosinolate metabolized by the myrosinase enzyme during mastication by the animal and the metabolites released into the bloodstream, thus making them available for deposition into either the animal's muscle or fat. This suggests that the metabolites resulting from the hydrolysis of glucosinolates in sheep may well be responsible for the "unacceptable" flavor in animals that consume forage rape prior to slaughter. This is, of course, speculative and requires substantiation. Nevertheless, it does provide an explanation as to why such an 'off-flavor' would be found in meat taken from brassica-fed animals.

EFFECT OF FEED SYSTEMS ON VOLATILE COMPOUNDS PRESENT IN COOKED SHEEPMEAT

Key volatile differences in cooked sheepmeat from grain- and pasture-fed systems reported in the literature are summarized in Table 2. For pasture systems, compounds such as terpenes and diterpenoids (volatile compounds present in the cooked meat) are derived from the feed.[8] 2,3-Octanedione is a common volatile compound found in the cooked meat from pasture-fed sheep and has been noted by Young et al.[8] to be an excellent indicator of pasture diet. Priolo et al.[61] have also substantiated this observation, whereas recent work has suggested that 2,3-octanedione would be a suitable biomarker for authentication of a pasture diet.[62]

Higher concentrations of γ-lactones have been associated with the use of grain feeding regimens for sheep.[49] Free fatty acids available in the grain are likely to be the precursors for these compounds[63] as these workers have suggested a mechanism for the biosynthesis of γ-dodecalactone from oleic acid. δ-Lactones have also been reported to be high in the meat obtained from pasture-finished animals[42] as well as in the milk obtained from pasture-fed cows.[63]

Diet has also been implicated with the formation of short-chain branched-chain fatty acids (BCFAs), which are regarded as the main contributors to the 'mutton' aroma in cooked sheepmeat. The most notable BCFAs have been 4-methyloctanoic (MOA), 4-ethyloctanoic (EOA), and 4-methylnonanoic (MNA) acids. Higher concentrations of these compounds have been observed in animals receiving a grain-based finishing diet prior to slaughter.[45,64−66] This has been attributed to greater availability of carbohydrate within grain-based diets relative to those that are pasture based.[15] On the basis of this observation, it might be logical to conclude that grain-dominated diets would result in increased 'mutton' flavor in the cooked meat, but Young and Braggins[77] have noted cereal grains differ in their propensity to generate BCFAs, so some care is required in extrapolating this observation. Additionally, higher levels of BCFAs (MOA, EOA, and MNA) have been reported in animals fed pasture finishing diets (native pasture, saltbush, or mixed lucerne) compared to those derived from grain feeding, but the reason for this was unclear.[67]

Table 2. Chemical Compounds Reported As Associated with Pasture- and Grain-Based Feeding Systems in Sheepmeat

volatile compound	tissue	ref
Pasture-Based Feeding System		
diterpenoids	fat	8, 62, 182
2,3-octanedione	fat	8, 61, 182
3-hydroxyoctan-2-one	fat	182
δ-lactones	fat	42
long-chain alkanes	fat	183
C7 aldehydes	fat	183
sesquiterpenes/terpenes	fat	61, 62
hexanoic acid	muscle	96
BCFA	fat	8
3-methylindole	fat, meat	8, 45, 96
phenols	fat, meat	96
toluene	fat	62
γ-lactones	fat	42
longer chain aldehydes (2-undecanal)	fat	8
Grain-Based Feeding System		
branched-chain and nonbranched fatty acids	fat	183
4-heptanone, 2-octanone	fat, meat	93, 184
3-hydroxy-2-butanone	muscle	96
alkenals, alkadienals, Strecker aldehydes, and ketones	muscle	104

Effect of Feed Systems on 3-Methylindole Production. 3-Methylindole ("skatole") and 4-methylphenol (*p*-cresol) have been implicated as the main volatile contributors to the 'pastoral' aroma evident in the cooked meat of pasture-fed sheep.[45] Pasture has a high ratio of protein to readily fermentable carbohydrate, and the protein from pasture is more readily digestible in the rumen compared to that available in grain and concentrate diets.[68] Additionally, substantial degradation of feed protein to amino acids occurs in the rumen, which allows a higher availability of peptides and amino acids that cannot be fully incorporated into microbial protein because insufficient energy is released from carbohydrate metabolism.[69]

3-Methylindole is formed in the rumen from the anaerobic metabolism of L-tryptophan.[70,71] Lush pasture is a rich source of readily degradable protein and is a potential source of tryptophan.[72] Indole, an associated metabolite, is also formed in the rumen, and, along with 3-methylindole, has a fecal odor. For 3-methylindole, tryptophan is transformed by rumen bacteria and protozoa in a three-step process (Figure 1A).[69,71,73] Initially, tryptophan is deaminated to form indolepyruvic acid, which undergoes two successive decarboxylation steps via an intermediate, indoleacetic acid, to form 3-methylindole.[70−72] Usually, 3-methylindole would be metabolized by the liver after release into the blood supply from the intestine. When in excess, though, some can escape liver metabolism and be released into the blood supply for deposition into fat tissue.[68,74] Both of these compounds are

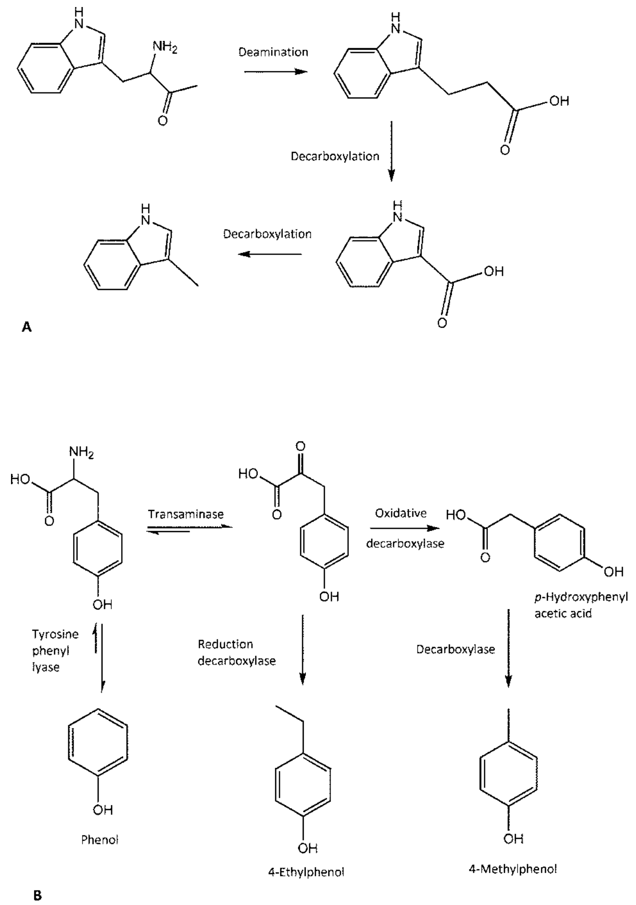

Figure 1. Biochemical synthesis for the production of (A) 3-methylindole from tryptophan (adapted from ref 69) and (B) 4-methylphenol and related compounds from tyrosine (adapted from ref 74).

lipophilic and so accumulate in the adipose tissue. It would also appear that diets high in protein, such as lucerne or clover, lead to an accumulation of 3-methylindole and indole in the rumen of sheep.[33] In the case of cattle, absorption can occur in the rumen,[68,70] whereas, for pigs (monogastrics), absorption of 3-methylindole occurs along the colon and it is then transferred to the liver as well as the circulating blood.[74] 4-Methylphenol is also produced by rumen bacteria from another amino acid, tyrosine.[72,75,76] Tyrosine undergoes successive transamination and decarboxylation steps to produce the intermediate, *p*-hydroxyphenylacetic acid, which then undergoes further decarboxylation to form 4-methylphenol (Figure 1B),[75] which can then be absorbed and transported by the blood supply for deposition into the fat tissue. The seasonal variability of a pasture's chemical composition also has implications for the production of the compounds related to 'pastoral' flavor. With higher total nitrogen concentrations in pasture over the winter period,[28] there is the implication that there could also be higher concentrations of 'pastoral' flavor related compounds as well, suggesting the presence of a temporal component associated with this flavor. By implication, the seasonal variation of the components in forage also suggests that there could be a seasonal component with sheepmeat flavor overall as well.

It is possible that the impact of 3-methylindole can be reduced by the inclusion of condensed tannins (CTs), a class of naturally occurring polyphenols present in certain forage legumes, into the feed systems.[72] CTs, which have been extracted from the forage legume *Dorycinum rectum* and added to mixed cultures of ovine rumen microbes, were found to inhibit the conversion of protein to 3-methylindole and indole by rumen microbes. In particular, the extracts inhibited the transformation of indoleacetic acid to 3-methylindole by rumen bacteria. Other workers employed sulla (*Hedysarum coronarium* L.), a legume that is another source of CTs, as a feedstock and reported that there was no effect of CTs on the concentrations of these compounds in the fat. This was largely attributed to the low CT content measured in the legume.[77] Further confirmation of the impact of CTs on the formation of indole and 3-methylindole was made using *Lotus corniculatus* as a feedstock for grazing lambs.[78] These workers found that lower concentrations of indole and 3-methylindole were present in rumen fluid and blood plasma taken from animals that grazed on *L. corniculatus* prior to slaughter compared to those grazed on ryegrass/white clover. A similar trend was found for 3-methylindole in fat samples. A trained sensory panel also evaluated the odor emanating from molten fat, taken from the animals off the two different feeding regimens, but found no discernible difference. These workers concluded that the reduction in indole and 3-methylindole concentrations due to CT was not sufficient to affect the odor from the heated fat. In fact, no significant difference between the mean indole concentration of the tail-stub fat was found for the two grazing treatments, and only a marginal effect was found for 3-methylindole ($P < 0.06$[78]). Thus, it is feasible that similar concentrations of these compounds were present in the intramuscular fat and thus were not detectable by sensory analysis, although this assumes that the concentrations of these compounds in the intramuscular fat are the same as those in tail-stub fat.

Quebracho (*Schinopsis loretzii*) is a hardwood tree, native to Paraguay, and is of commercial importance because of its tannin content. Quebracho tannins, in the form of a powder extract made from tree bark, have been added to forage- and concentrate-based sheep feeding systems, and the production of 3-methylindole has been reduced in animals from both production systems.[79] Comparatively, the tannins were more effective in reducing 3-methylindole production in sheep fed the concentrate feed systems compared to those fed forage. Depending on the extract's protein content, a plausible explanation is that the tannins may form complexes with proteins which make them unavailable for subsequent transformation to 3-methylindole. This is speculative and needs to be confirmed but, if true, the impact of pasture on cooked sheepmeat could be ameliorated by using feed with high CT concentrations.

Grape seed extract (GSEs) are another source of CTs and have been used to dose animals fed diets of white clover and perennial ryegrass. The use of GSE resulted in only small reductions in indole and 3-methylindole concentrations in rumen fluid and blood plasma as well as odor scores in associated fat samples.[80] In separate work, CTs were added as an oral supplement (prepared as extracts from *Lotus pedunculutus,* a perennial common in Europe, and grape seeds) and shown to reduce the formation of indole and 3-methylindole in the rumen.[81] In addition, the CT content of forage has been shown to be a factor that affects the formation of these compounds because plants with higher CT concentrations tend to be more effective in reducing the production of these compounds in the rumen.[82]

Effect of Protected or Unprotected Lipid Supplementation. The use of oil supplementation to feed systems as a means of incorporating higher levels of fatty acids of nutritional value, such as linoleic acid (C18:2), into ruminant milk and body fats was initially reported in the mid 1970s.[83] Protection of the supplement from ruminal hydrogenation was obtained by encapsulating oil droplets in protein that was then treated with formaldehyde to prevent breakdown in the rumen. The use of a lipid-protected sunflower oil supplement, for example, has been reported to increase the linoleic acid component of the total fatty acid content (up to 30%) of meat taken from lambs fed on the supplement.[83] A 'sweet-oily' aroma was reported in the cooked meat of the product, and the source of the 'sweet' aroma was identified as γ-dodeceno-6-lactone, whereas *trans,trans*-2,4-decadienal, an oxidation product of linoleic acid (C18:2 n-2), was implicated as the contributor to the 'oily' aroma note.[83] Similar observations were reported for dairy cattle where the lactone was present in butterfat extracted from the milk taken from these animals that had been fed the same supplement.[84] Later work, using a trained sensory panel, reported that an unacceptable flavor was found in meat taken from animals fed on the supplement over a period of 6 weeks, and this flavor note increased in intensity with the length of the experiment.[85] A corresponding increase in the level of γ-dodecen-6-lactone was also reported for the meat samples, which was reported to be the main contributor to the unacceptable flavor.[85] The use of the protected sunflower oil supplement was suggested as being suitable for ameloriating the impact of 'mutton' flavor. Meat taken from pasture-fed animals that had received 1−2 weeks of treatment of the sunflower oil supplement was found to have a small but significant decrease in mutton aroma and flavor intensity that was not evident in the meat taken from lot-fed animals. It should be noted that when this study was reported, little was known about the impact of diet on sheepmeat flavor. Thus, it is possible that the panel was detecting 'pastoral' flavor associated with cooked meat from the pasture-fed animals and that the difference detected by the sensory panel was related to the feed systems and not to the use of the supplement.

More recently, attention has been given to other polyunsaturated fatty acids (PUFAs), namely, α-linolenic (C18:3 n-3), eicosapentaenoic (EPA, C20:5 n-3), and docasahexaenoic (DHA, C22:6 n-3) acids, and their impact on the volatile aroma compound profiles found for cooked and grilled lamb meat.[47,86] For cooked meat, higher levels of lipid oxidation products were found in product derived from lambs fed a supplement based on fish oil, a rich source of EPA and DHA.[47] Notably, levels of unsaturated aldehydes, unsaturated hydrocarbons, and alkylfurans were up to 4-fold higher compared to the control and resulted from the oxidation of PUFAs during cooking. Although no sensory evaluation of the cooked meat was performed in this study, presumably the use of fish oil as a dietary supplement would affect the sensory properties of the cooked meat.

This was later substantiated with a comparative study on the use of marine algae and fish oil, both good sources of EPA and DHA, compared to the use of a protected sunflower oil supplement (similar to the one made by Park and co-workers mentioned above) for feeding lambs.[86] Elmore and co-workers[86] measured the volatile profiles of grilled lamb from the different feeding regimens. Higher levels of oxidation products from n-3 fatty acids were found for the meat from the lambs fed fish oil/algae diets, whereas compounds derived from n-6 fatty acids were highest in the meat from the lambs fed the protected lipid supplement. Interestingly, these authors did not give the results but only commented on the sensory profiling of the grilled lamb samples and noted that less than desirable scores were associated with the meat derived from the diets based on the fish oil/algae diets. Fishy odors were reported for the meat samples derived from the diets containing fish oil, and abnormal and rancid flavors were found for the animals fed the algal diets. Elmore et al.[86] also noted that, although increasing the concentration of these PUFAs in muscle may be nutritionally desirable, poor sensory quality could also result if the PUFA levels were excessive. Recent work with kid goats confirms this observation as high levels of DHA were added as a supplement to a preslaughter diet to manipulate the fatty acid profiles of goat muscle, resulting in a meat product with unusual odors, unpleasant flavors, and low overall sensory appreciation scores.[87] Clearly, the use of oil supplementation to the diet can improve the nutritional aspects of the final product, but it also reduces the cooked meat quality and acceptance by consumers.

Clearly, the effect of the feed system, whether as simple feed (such as pasture or grain) or as a supplement, on the volatile compounds in cooked sheepmeat is neither simple nor straightforward, and further work is needed to elucidate what is a complex relationship between the feed system and the volatile composition. The complexity of this relationship is demonstrated by the study of Bailey et al.,[42] in which multilinear regression was needed to relate volatile chemical composition to 'grassy' and 'lamb' flavor intensities in cooked sheepmeat.

AN INTEGRATED VIEW OF THE EFFECT OF FEED SYSTEMS ON LAMB FLAVOR

The mechanisms by which feed can affect final lamb flavor are complex and multiple. In its simplest form, feed may affect the final flavor of lamb by direct transfer of specific plant-derived compounds into the meat, which may then impart specific flavor notes. For example, phytol, phytene, terpenes, and sesquiterpenes (all derived from pasture) may accumulate within the muscle tissue.[61,88] Once within the sheepmeat, these compounds may directly affect the final flavor if present at sufficient concentration, or they may undergo degradation during thermal processing to form new flavor-active compounds.

The composition and fatty acid profile of meat can be affected by feed.[14] During cooking, extensive oxidation reactions result in potent lipid-derived odor-active volatile compounds. These oxidation pathways are affected by the initial types of fatty acids present (pattern of unsaturation), meat pH, antioxidant status (presence of α-tocopherol and carnosine, etc.), and also the presence of heme and nonheme iron.[89,90] Different fatty acids will produce different odor-active volatiles as a result of the oxidation induced from the temperature used to cook the meat. Significant diet-induced changes in the initial fatty acid profiles influence the type and quantity of volatiles produced.[90] Even if there are no differences in the volatile composition, changes in the relative ratios of lamb aroma compounds, or an atypically high concentration of a few volatiles, may result in noticeable sensory differences in the final cooked meat, although no unique feed-specific volatile molecules may be present.

A specific feed type may affect the final fat content and distribution of intramuscular saturated and unsaturated lipid.[14]

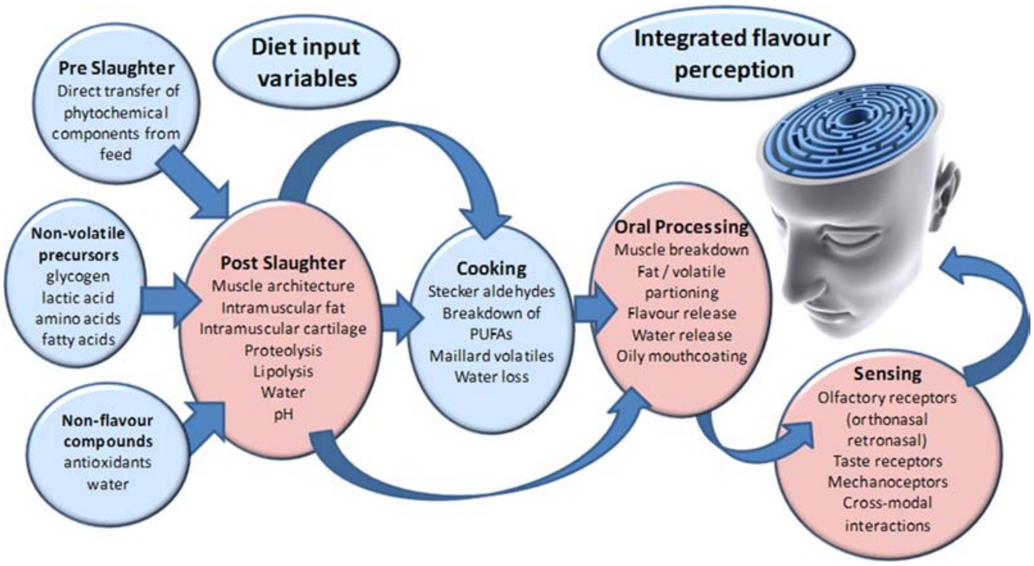

Figure 2. Diagrammatic summary of important variables where the interactions of feed and processing may directly or indirectly affect the final flavor attributes of lamb (meat) and perception.

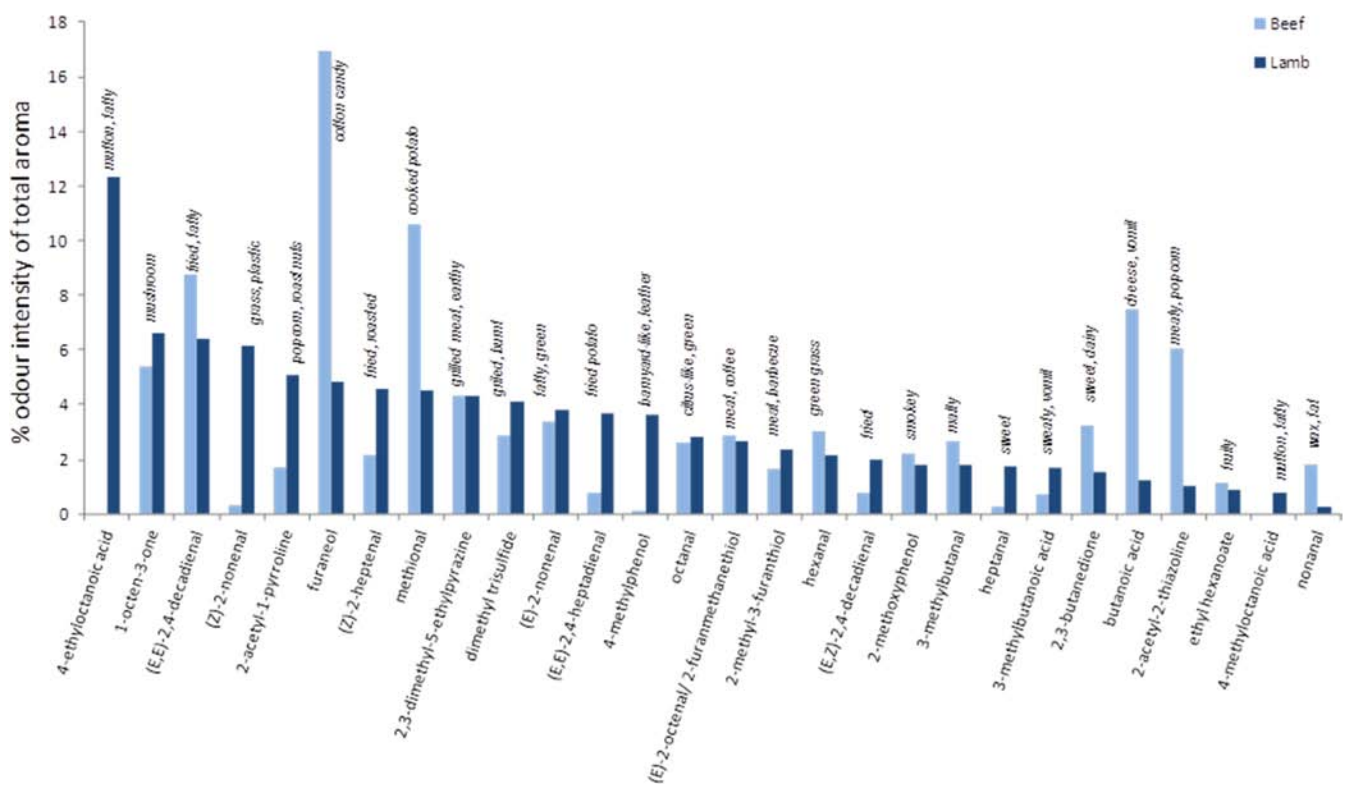

Figure 3. Composite aromagram based on a meta-analysis of recent literature on GC-O data from lamb and beef meat aroma studies. Data from individual studies were scaled to a percent of total aroma stimulus before averaging. Lamb volatiles are listed in order of decreasing odor impact.

Apart from effects on texture, an increased meat fat content will act as a reservoir for lipophilic volatile compounds directly affecting the rate and extent of release during oral processing. Although not extensively demonstrated in meat systems, the presence of fat has been shown to attenuate the release of volatiles from emulsions, thereby increasing the relative amount released postswallow compared to preswallow.[91−93]

Lamb Meat Flavor. To understand flavor differences that may be affected by feed and pasture, it would be helpful to have an objective understanding of the essential components required for "characteristic" or baseline lamb flavor (see Figure 3). Integrated flavor perception is brought about by the interaction of nonvolatile and volatile (meat) components with human chemosensory receptors, including taste and olfactory receptor cells as well as other sensory networks (see Figure 2). Textural components, such as tenderness, juiciness, chew resistance, muscle structure, and breakdown may also directly affect or attenuate overall perceived flavor. The overall content and intramuscular distribution of fat within the muscle structure may also play an important role in the way flavor compounds are released and perceived. Extraction and quantitative measurement of volatile compounds can be challenging but more straightforward than measurement of nonvolatile components. There is no single analytical technique that can separate and quantitatively measure the nonvolatile components of meat flavor (free amino acids, flavor nucleotides, peptides, fat globules, free fatty acids, sodium ions, etc.[94]). Multiple analytical approaches are needed to comprehensively describe the nonvolatile composition.

Measurement and quantification of nonvolatile flavor compounds are more analytically demanding, and it is for this reason these compounds are often overlooked with the focus placed on volatile flavor compounds. The relative contribution of both nonvolatile and volatile molecules to the final sensory attributes is debatable; however, it is probable that significant cross-modal interactions exist, and multisensory processes are required for integrated flavor perception.[95] It is clear that both nonvolatile and volatile compounds need to be present in the right concentrations and at the appropriate ratios to create desirable flavor attributes. Measurement by gas chromatography−mass spectrometry (GC-MS) is the usual approach to characterize the complex volatile composition of lamb or mutton aroma. Numerous studies have produced extensive lists of volatile compounds measured in the headspace of lamb samples[47,96] or beef samples;[97,98] surprisingly few published studies have determined the odor activity values (OAVs) or sensory relevance of specific volatiles within lamb or meat volatile extracts. The OAVs are calculated from the ratio of the concentration of a volatile in the sample headspace to the accepted olfactory recognition threshold for the same compound in a similar matrix.[99] When the OAV is <1, it is unlikely that a volatile compound has an impact on the overall aroma. As the OAV increases for a volatile component, the probability that it contributes to the overall aroma increases. An estimate of the odor contribution of individual molecules may be obtained by ranking OAVs; those with the highest values normally make the largest contribution to the aroma. A significant problem with this approach is the lack of availability of reliable threshold values for odor compounds of interest in relevant chemical matrices. A more reliable, but time intensive method of ascertaining the sensory relevance of volatiles is the technique of gas chromatography−olfactometry (GC-O). Using a direct intensity or a dilution method, odor-active volatiles can be identified and ranked in relative importance. Volatile extracts are subjected to chromatographic separation and instrumental detection by either flame ionization detection (FID) or mass spectrometry (MS), the gas effluent is simultaneously sniffed by human assessors, and the odor intensity is rated. Despite many published works on the volatile constituents of lamb and other meats, few studies include comprehensive sensory-directed flavor analysis.

■ META-ANALYSIS OF GC-O MEASUREMENTS OF COOKED LAMB MEAT AROMA

The purpose of GC-O is to discriminate between odor-active and non-odor-active volatiles and assign a relative odor-intensity or impact value to individual volatiles, which then allows for the identification of a subset of volatile compounds that might have a significant odor impact. In any aroma characterization, the validity of the findings will depend strongly on the extraction method employed and of course the dietary history, the age of the meat, the cooking methods used, and other factors. Common volatile extraction methods include high-vacuum distillation,[100] purge and trap methods with Tenax,[86,90] solid phase microextraction,[101] and dynamic headspace extraction with solid phase extraction with subsequent solvent elution,[102] all of which have been applied to characterize meat flavor.

Each extraction method produces different results. Similarly, results may also vary depending on the olfactometric method used, for example, dilution or direct intensity method. Direct intensity GC-O methods rate the relative intensity of the odor stimulus using a sensory scale (e.g., 100 mm computerized line scale); normally a panel of assessors or "sniffers" is employed. Dilution methods can also be used, during which an aroma extract is serially diluted and assessed multiple times. Odors that can be detected after a greater number of dilutions have higher flavor dilution values (FDV) and normally make a relatively greater contribution to the aroma or have a greater odor impact.

GC-O allows a degree of data reduction, whereby volatiles with odor activity or sensory relevance can be identified. In practice, the number of odor-active volatile compounds is always considerably less than the number of volatiles identified by GC-MS. For example, Elmore et al.[47] measured more than 180 volatiles in the headspace of cooked lamb samples. Of these, more than 60 were sulfur-containing compounds. In another study more than 70 sulfur volatiles were reported.[98] However, despite these impressive lists, GC-O experiments have shown that only a small number of them are likely to have sensory relevance, including methanethiol, 2-methylthiophene, 2-methyl-3-furanethiol, dimethyl trisulfide, methional, methionol, and 2-acetyl-2-thiazoline.[98]

In the recent literature, few lamb-specific GC-O studies have been published. Around 45 odor-active volatiles were identified in lamb headspace extracts in ref 103, whereas only 20 were reported using a similar approach by Resconi et al.[104] In an aroma extract dilution analysis (AEDA) study (where the importance of an odorant is determined by dilution[105]) on cooked lean lamb meat aroma, only 15 compounds (principally aldehydes) were reported with FDVs over 128,[106] indicating the significance of these odorants. Even for beef aroma, surprisingly few comprehensive GC-O studies have been published; 25 odor-active compounds were identified by AEDA in roast beef extracts,[107] 16 in stewed beef juice,[108] and 48 by AEDA in beef gravy,[100] and more than 40 were reported by Resconi et al.[102] using a headspace volatile extract method

Despite numerous GC-O studies, a universal consensus is lacking on which volatile components are essential to produce lamb (meat) aroma. As extraction methods and olfactometric approaches have inherent biases and GC-O experiments are expensive and time-consuming to conduct, a rational approach to summarizing and building on existing published information would be useful. Similar in concept to meta-analysis of randomized clinical trial data, we propose the concept of a "meta-aromagram", building on published GC-O data to obtain a picture of generic or baseline aroma for any food product of interest, in this case, specifically, lamb flavor. The essential differences in the aroma of lamb and other red meats, for example, beef, could be more rationally understood using this approach. As new GC-O data are published for lamb aroma, they can be added to the existing body of knowledge. As researchers positively identify and confirm the role of existing compounds in lamb aroma extracts, the more certain we can be of their generic importance, and the greater influence they will

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have in the meta-aromagram and, hence, be considered a core component in lamb flavor. Conversely, for compounds that are described in only specific studies, we can assume the volatile is an artifact, misidentified, or, depending on its FDV or intensity, a compound very specific to a feed-specific component. In the latter case, one could apply a reverse engineering approach to identify the most likely precursor compound in the feed.

A meta-aromagram of recently published meat GC-O literature was conducted. Data from recent lamb GC-O[103,104,106] and beef studies[100,102,107,108] were compiled. Olfactory data were converted to a common percentage scale of total rated stimulus before averaging. With the exception of the BCFAs (MOA and EOA) identified in sheepmeat extracts in ref 106, compounds identified in only one study but not the others were removed. The average stimulus across each of the lamb and beef studies was calculated on the basis of the top impact compounds for lamb and beef (Figure 3). The volatiles were ordered in decreasing rank order based on the lamb volatile data.

On the basis of the lamb aroma meta-analysis, the top 15 impact compounds in lamb baseline aroma were identified in decreasing rank as 4-ethyloctanoic acid (*mutton-like*), 1-octen-3-one (*mushroom*, *earth*), (*E*,*E*)-2,4-decadienal (*fatty*, *fried*), (*Z*)-2-nonenal (*plastic*, *chlorine*), 2-acetyl-1-pyrroline (*popcorn*, *roasted*), Furaneol (*caramel*), (*E*)-2-heptenal (*fish*, *fried*), methional (*cooked vegetables*, *potato*), 2,3-diethyl-5-methylpyrazine (*nutty*, *roasted*), dimethyl trisulfide (*sulfur*), (*E*)-2-nonenal (*cardboard*, *wood*), decanal/2,4-(*E*,*E*)-heptadienal (*roast meat*, *potato*), 4-methylphenol (*stable*, *animal*), octanal (*lemon*, *floral*), and (*E*)-2-octenal (*grass*). The aroma descriptors were taken from the cited GC-O studies. The relative impact and rank order of compounds in the beef meta-aromagram were quite different from those of lamb. For example, 4-ethyloctanoic acid is absent from beef profiles; Furaneol, methional, butanoic acid, and 2-acetyl-2-thiazoline were of greater relative importance in beef aroma extracts and 4-methylphenol, less. Of these compounds, 4-methylphenol is formed from tyrosine present in the pasture or feed. Depending on whether animals are predominately pasture- or grain-fed, this compound will make a differing contribution to the final aromagram. For example, beef and lamb in Australia are mainly pasture-fed[3,109] whereas U.S. beef production is predominately based on the use of feedlots.[110] Thus, the differences in the feeding systems may be responsible for the differences observed in the aromagram. As described earlier, high-protein pasture commonly used in lamb feed often has high tyrosine content; thus, the greater aroma activity of this compound in the lamb is logical. The greater relative importance of fat-derived volatiles in the lamb meta-aromagram also may represent a general difference between lamb and beef aroma. The remaining impact odor compounds present in the lamb aromagram were derived from either Maillard reactions or Strecker degradation of amino acids; for example, methanethiol, dimethyl trisulfide, and methional derive from methionine,[111] 2-acetylpyrroline derives from proline,[112] and 2-methyl-3-furanthiol and 2-acetyl-2-thazoline derive from cysteine and ribose.[113,114] These compounds are formed from nonvolatile and semivolatile precursors, which are transformed by thermal processing, rather than being transferred directly into the meat. Diet directly affects the free amino acid and fatty acid profiles (often the precursors for Maillard reactions and/or Strecker degradation) of the meat potentiating formation of these volatiles.[115] Many of the lower impact volatiles in the meta-aromagram are generated via oxidation of unsaturated fat or amino acid degradation. It should be emphasized that BCFAs were not identified as odor-impact compounds in most of the lamb GC-O studies described above except for ref 106; this is attributed to the fact that lean meat was used. It is known that BCFAs are largely present in the lamb fat and increase with animal age.[67] Obviously, more robust GC-O studies are required directed at lamb specifically, especially to clarify the role of BCFAs in lean lamb flavor. Such studies will lead to a better understanding of the volatile signature of quality lamb aroma and the impacts that changes in diet have on meat flavor.

FLAVOR RELEASE

Flavor and perception have important temporal components that are influenced by the composition and structure of food and oral processing.[116] This applies to both nonvolatile (e.g., salt,[117−120] amino acids[121]) and volatile aroma compounds. The timing, rate, and amount released from the food matrix are thus an intrinsic part of the sensory properties of a food. The presence of fat, for example, has a singularly profound effect on the release of volatiles.[91,122] Other food components such as protein, peptides,[123] carbohydrates,[124] and saliva components[125] have also been shown to affect release. Meat is largely composed of protein (16−22%), water (75%), and fat (3−7%).[126] The unique structure of muscle meat adds another layer of complexity, with muscle fibers, fat globules, and intra- and intercellular water creating a unique flavor delivery matrix. During oral processing (mastication), the breakdown of muscle fiber and connective tissue, and subsequent release of flavor form part of the unique sensory characteristics of meat. The ability of skeletal muscle dipeptides (carnosine and anserine) and sarcoplasmic protein (e.g., myoglobin) to interact with volatiles and affect their release has been demonstrated in two studies.[101,127] Fat has the capacity to act as a solvent for volatile compounds, and its role in the release of these compounds in meat products has also been investigated.[88,117,128,129] Volatile release has been measured by GC and olfactometry in frankfurters with different fat contents (5, 12, and 30% fat).[88] In low-fat frankfurters, the volatile release of certain terpenes, sesquiterpenes, and phenols was significantly increased compared to the full-fat product, leading to greater perceived smoky and spicy odors. In a separate study, a higher intensity of mushroom aroma was perceived in low-fat bologna sausages, and the perceived juiciness was significantly higher and had longer duration in high-fat variants.[118] Higher levels of fat can reduce the release of volatiles, but the time to reach maximum concentration in the mouth (T_{max}) is not affected.[129] Further in vivo studies of mastication in the mouth using meat systems are required to understand implications for flavor development and perception. Dietary changes that affect the type, amount, and distribution of fat within animal muscle (i.e., IMF) must be considered as having the potential to significantly affect the final flavor and sensory quality of meat.[118,130] In a study comparing pork loins with high and low IMF, volatile compounds derived from lipid oxidation, such as 1-hexanal, octanal, (*E*,*E*)-2,4-heptadienal, and (*E*)-2-decenal, as well as amino acid derived products such as dimethyl sulfide, 3-methylbutanal, or phenylacetaldehyde, were significantly higher in the headspace from high IMF samples.[118]

Table 3. Taste Compounds in Sheepmeat[a]

compound	taste/other complex sensation
organic acids/salts	
lactic, acetic, and propanoic acids	sour
short-chain fatty acids, C_{4-10}	sour, soapy
propanoic acid	sour, umami
succinic acid	umami
Ca/Mg salt of propanoic acid	sweet
sugars/reducing sugars	
glucose/glucose-6-phosphate	sweet
fructose/fructose-6-phosphate	sweet
mannose, ribose	sweet
L-amino acids	
Gly, Ala, Ser, Thr	sweet
Glu, Asp, Gln, Asn	sour, umami
His	sour (?)
Pro, Lys	sweet, bitter
Leu, Val, Ile, Arg, Phe, Tyr, Trp	bitter
Met	sulfurous, meaty, slightly sweet
Cys	sulphurous
Lys, Arg	enhance salty taste
peptides	
hydrophobic peptides (∼2−12 amino acids)	bitter
β-alanyl-L-histidine (carnosine)	sour/mouthfeel at pH ∼5.7
	sweet/stronger mouthfeel at pH 6.8−7.6
β-alanylglycine	sour/slight astringent
	thick-sour orosensation/meaty
β-alanyl-*N*-methyl-L-histidine (L-anserine)	sour/slight astringent
	thick-sour orosensation/meaty
γ-glutamyl di- and tripeptides	sour, salty, brothy, metallic
arginyl dipeptides (Arg.Pro, Arg.Ala, Ala.Arg, Arg.Gly, Arg.Ser, Arg.Val, Val.Arg, and Arg.Met)	salt taste modulating peptides
nucleotide	
5′-AMP, 5′-IMP, 5′-GMP, 5′-CMP[b]	brothy, umami
other N-containing compounds	
creatine, creatinine, hypoxanthine	bitter
thiamin	brothy, meaty

[a]Compiled from refs 94, 138, 144, 148, 150, and 185−187. [b]AMP, adenosine-5′-monophosphate; CMP, cytidine-5′-monophosphate; GMP, guanosine-5′-monophosphate; IMP, inosine-5′-monophosphate.

■ MEAT TASTE COMPOUNDS

Until recently, little work has been reported that describes research into the presence of taste compounds in lamb meat and, more generally, in meat. However, this trend is changing as interest in this area increases. In the past, researchers have identified hundreds of volatile aroma compounds but relatively fewer nonvolatile taste compounds, paying little, if any, attention to the contribution that these compounds have made to the overall product flavor. Yet, over the past decade, sensory-directed fractionation of food extracts involving membrane separation and various liquid chromatography techniques, in addition to analytical sensory tools, have enabled the identification of taste-active lead molecules in foods. In food systems such as meat, it is also often difficult to study taste compounds in isolation of the matrix as this neglects the contribution made from the volatile aroma compounds well as the one made from the matrix itself, in terms of both the number of food constituents and their competing/synergistic effects on taste and/or aroma.

Additionally, because there has been growth in the development of research in this area only recently, compared to the research in aroma compounds, there is a paucity of literature that describes taste compounds present in lamb meat. Thus, for the purposes of this review, more general examples of taste compounds present in related food sources (such as muscle food/meats from poultry, fish/seafood, and mammals) have been identified and discussed in this section. It is reasonable to assume these compounds will also play similar and important roles in the taste of lamb meat as well.

There are a number of compound classes that potentially can contribute to the taste of meat and related products; the most notable are (i) organic acids (e.g., lactic and succinic acids), (ii) compounds derived from lipid precursors (e.g., short-chain acids), (iii) sugars (e.g., glucose and fructose), (iv) peptides and free amino acids produced from enzymatic hydrolysis of muscle proteins, (v) nucleotides, and (vi) Maillard reaction products. Of these categories, it has been largely recognized that low molecular weight, water-soluble compounds (namely, sugars, amino acids, and other nitrogenous components) are important as (a) background basic taste attributes (sweet, sour, salty, bitter, and umami)/complex orosensation such as mouthfulness and mouthfulness enhancing and (b) precursors of the characteristic aroma (meaty flavor) of cooked meat.[115,131,132] Production factors such as diet, breed, species, and post-mortem conditioning also have an impact on the concentration of taste compounds and flavor precursors (e.g., fatty acid profile, antioxidant content, and water-soluble flavor precursors) in ruminant meat.[104,115,133−136] Specifically, in the context of this review, higher levels of free amino acids in beef were associated with a pasture diet compared to grain.[115] It is likely that this will be the case with sheep as well.

A summary of relevant compounds, and their contribution to taste, is shown in Table 3. Lactic acid is the principal organic acid in meat produced by anaerobic conversion of glycogen, resulting in a pH decrease.[137] Its production and concomitant drop in pH are very much dependent on muscle type as well as glycogen concentration at slaughter. Other acids (such as acetic, propanoic, and C_4−C_{10}) will also contribute to the sour/soapy taste, but their major principal contribution is to meat aroma. The flavor intensity of short-chain fatty acids depends not only on the concentration but also on the distribution of these compounds between the aqueous and fat phases, the medium pH, the presence of certain cations (such as Na^+ and Ca^{2+}), and protein degradation products. The pH has a major influence on the flavor impact of short-chain fatty acids[138] as, at the pH of meat (~5.7), a considerable portion of free fatty acids are bound as nonvolatile salts, which reduces their flavor impact. Other organic acids (such as acetic, propanoic, lactic, succinic, and glutamic) whether in the free form or bound as ammonium, sodium, potassium, magnesium, and calcium salts, as well as corresponding chlorides and phosphates, have been reported to elicit taste notes such as sour, sweet, and salty in meat.[139]

Sugars (glucose, fructose, mannose, and ribose) have been detected and quantified in beef, lamb, and pork muscle, before and after heat treatment.[131,132] Ribose was reported to be the most heat-labile sugar, and fructose was the most stable of the sugars that were identified. The sugar phosphates, glucose 6-phosphate and fructose 6-phosphate, have been also been reported in an aqueous beef extract.[139] The sugar phosphates contribute to the sweet taste note in meat and also have been identified as precursors of important meat odorants via the Maillard reaction.[107]

Proteins in lamb meat can be hydrolyzed by native proteolytic enzymes (primarily by cathepsins and calpains) during storage/aging, which results in the production of peptides of various molecular weight/chain length and free amino acids. The precise role of these intermediate to small molecular weight peptides is not clear, but it is generally accepted that they contribute to the background taste of meat.[140,141] Proteolytic degradation of muscle protein also has major consequences for the textural characteristics, water-holding capacity, and possibly release of flavor/taste components as well. The vast majority of peptides produced in meat have no characteristic taste of their own but enhance the basic taste in combination with other compounds such as glutamic acid and 5′-nucleotides. Numerous specific peptides have been identified as bitter, beefy/meaty/brothy, salty, sour, and umami (Table 3).

Amino acids also contribute characteristic taste notes to meat. The taste quality of L-amino acids, which are the building blocks of proteins, depends on the structure of the side chains (see Table 3). In contrast, most of the D-amino acids, formed either by bacterial degradation or by processing, are predominately sweet, and their taste quality is largely independent of the side-chain structure.[142−144] The magnitude of umami taste is synergistically enhanced with the presence of umami amino acids (acidic L-amino acids, e.g. aspartame (Asp), glutamic acid (Glu)) and umami nucleotides.[144] An important characteristic of umami taste is its ability to enhance flavor. This key phenomenon can be employed in foods in general to reduce salt intake.[145,146] In beef juice, 47 taste-active compounds were identified but, using trained sensory taste panels, this number was narrowed down to 17 low molecular weight compounds as important to the overall taste.[94] These compounds included organic acids (lactic and succinic acids), amino acids (alanine, Glu, Asp, and cysteine), dipeptides (carnosine), 5′-nucleotides (adenosine-5′-monophosphate (AMP), cytidine-5′-monophosphate (CMP), guanosine-5′-monophosphate (GMP), and inosine-5′-monophosphate (IMP)), N-containing bases (creatinine, creatine, and hypoxanthine), and sodium, potassium, magnesium, chloride, and phosphate salts. Two 5′-nucleotides in combination with amino acids (Glu and Asp) were primarily responsible for the taste attributes brothy/umami of meat juices, whereas organic acids (lactic and succinic acids) and salts (sodium, potassium, magnesium, chloride, and phosphate) contributed to the salty, sour, and umami tastes, also. The 5′-nucleotide compounds (AMP, CMP, GMP, and IMP) occur in many savory foods such as meat, fish, seafood, and mushrooms.[147]

Low molecular weight peptides have been characterized and shown to elicit a wide of range of taste notes and other complex sensations; for example, cyclic dipeptides have been reported to contribute to the bitter taste,[148] whereas γ-glutamyl dipeptides have been found to be contributors to a variety of tastes (sour, brothy and slightly sour, salty, and metallic).[149] Other peptides are reported to add to more complex taste sensations; γ-glutamyl peptides for enhanced kokumi sensation induce mouthfulness, thickness, and a long-lasting taste sensation;[121] β-alanyl dipeptides contribute to mildly sour and astringent and thick-sour mouthfeel and the white-meaty character of chicken broth;[148] and arginyl peptides were reported to modulate salt taste[150] (see Table 3). As noted above, the amount of research that has investigated the role and impact of taste compounds on the overall flavor of cooked sheepmeat is comparatively lower than that published relating to aroma compounds resulting from the cooked product. Further work is needed to quantify what taste compounds are present in the cooked product as well as elucidate the contributions made by these compounds to the overall flavor in addition to the impact that feed systems have on the taste compounds.

■ INDIRECT FLAVOR EFFECTS

Any changes in diet that affect the final protein or antioxidant status of muscle derived from sheep can also theoretically affect the final flavor characteristics. Carnosine is the most abundant dipetide in sheep skeletal muscle and has antioxidant activity.[151] The histidine-rich compound has been to shown to decrease lipid oxidation and minimize formation of odor-active aldehydes and other Maillard volatiles.[9] The same compound also has a positive influence on the thermal generation of pyrazines, which are significant contributors to the overall perceived meat aroma in general.[152] Diets high in β-alanine and histidine may increase the final carnosine content and antioxidant potential of meat,[153] theoretically reducing lipid-derived volatiles forming during cooking. The presence of particular metal ions (e.g., Cu and Fe) can affect the rate of lipid oxidation, resulting in elevated aroma volatiles.[89,154] Differences in diet can affect other factors that will influence the overall flavor characteristics of the final meat product. For example, meat from concentrate-fed animals underwent lipid oxidation more readily compared with meat from pasture-fed animals while stored in refrigeration for 7 days under gas permeable film.[36]

Vitamin E is an essential dietary vitamin for sheep because it is not made by the rumen or animal and it assists with animal growth, reproduction, and protection of tissue integrity.[155] Green forage and other leafy materials are very good sources of vitamin E, with concentrations in fresh herbage 5−10 times higher than in some cereals (also an abundant source).[155] The freshness of herbage is of paramount importance, though, because processing causes considerable vitamin E losses. The influence of diet (and thus vitamin E) on lipid oxidation of lamb meat has been studied by Santé-Lhoutellier et al.,[36] who reported that meat taken from pasture-fed lambs was oxidatively more stable compared to the meat taken from concentrate-fed lambs. The lipid oxidative stability of the meat was noted to be due to the higher vitamin E levels in pasture compared with that found in the concentrate.[36]

Diet could also have an effect on the concentrations of water-soluble precursor flavor compounds in sheep meat. This has been observed in beef,[115] where pasture feeding was found to increase free amino acid levels, compared to beef taken from concentrate-fed animals, whereas concentrate-fed animals had higher levels of reducing sugars (i.e., those sugars which can act as reducing agents). Similar water-soluble precursor compounds have been found in goat meat,[156] and so it is likely that this will be the case for sheep as well. The fatty acid composition of lamb meat can also be modified with diet.[157]

■ SHEEPMEAT FLAVOR IN THE CONTEXT OF MUSCLE QUALITY AND GENETICS

Dark-cutting in muscles of the sheep carcass is a quality defect that occurs worldwide and, in some countries, is called dark, firm, and dry (DFD).[158] In the context of this review, dark-cutting meat has a bland flavor, due most likely to the lack of glucose in the muscle[159] and ultimate pH.[160] Dark-cutting is due to low muscle glycogen levels at slaughter, which directly affects the ultimate pH of the carcass. Importantly, in the context of this review, preslaughter nutrition of the animal influences the muscle glycogen levels at slaughter.[20,161] As a general rule of thumb, if sheep are gaining weight at 100 g day^{-1}, the levels of muscle glycogen at slaughter will be sufficient to prevent the occurrence of dark-cutting.[162] The Merino breed of sheep that dominates Australian and New Zealand production is more susceptible to exhibiting dark-cutting[163] and so is recommended to have a preslaughter weight gain of 150 g day,$^{-1}$ [158] although there is a large variation within and across breeds.

Marbling is a visual score given to a piece of meat, defining the amount of visible flecks of fat within the meat, whereas intramuscular fat (IMF) is the chemically measured fat content (which includes membrane lipids), although these terms are often used interchangeably. The term, marbling, originates from the beef industry and is considered to be highly desirable in the United States to achieve tenderness and desirable flavor and juiciness.[164] Sheep meat tends to have little visible marbling when compared to similar IMF levels found in beef.

The effect of IMF on the objectively measured tenderness (shear force) of meat from lamb carcasses has been investigated,[32,164] and higher IMF levels have been found to be associated with more tender meat. IMF levels in lamb loin, over the range from 2 to 18%, have been shown to influence the consumer acceptability of lamb flavor, with higher IMF corresponding to a more acceptable flavor in the sheep meat.[30] The heritability of IMF and tenderness in the sheep population and the main influencing factors have been investigated.[32,165,166] To date, though, there are no available data on the heritability of sheepmeat flavor or odor; the only available information is more general in nature and discusses overall sheepmeat quality.[167,168]

The meat from progeny of sheep sires that are extreme in either muscling or fatness have been found to produce meat that is unacceptable to the consumer via changes in tenderness (proteolysis, connective tissue) or juiciness/flavor (probably via influence on IMF), and it is recommended that such sires should be avoided.[169,170] Thus, it may be important to consider the variations in the flavor and acceptability of lamb meat from different genetic lines.

In addition to the low availability of data relating to the heritability of flavor or odor, very few data are available on the heritability of the relevant compounds known to be associated with sheepmeat flavor, for example, BCFAs, 4-methylphenol, and 3-methylindole (see above). Some evidence does exist on the impact of breed on the levels of BCFAs (MOA and MNA) where higher levels of these compounds have been found in the subcutaneous fat taken from Poll Dorset × Merino animals compared to other genotypes.[170] Additionally, sensory panels have observed flavor differences in the cooked meat taken from different breeds of sheep.[171,172] Although there have been reports of differences in meat flavor between breeds, Duckett and Kuber[173] concluded that the finishing system was more important than breed in determining lamb flavor.

■ CONSUMER PERSPECTIVES OF SHEEPMEAT AND SHEEPMEAT PRODUCTS

As noted in the Introduction, a number of countries in the world, especially in arid Mediterranean and arid climates, are involved in sheepmeat production either for their own domestic consumption or for export to overseas markets. It may be safely assumed that in all of these countries a significant fraction of the native population is accustomed to, and accepts, the characteristic flavor of locally produced sheepmeat as "normal", whether cooked and eaten as primal cuts or used as an ingredient in processed foods. These populations of consumers can be described as habituated to the local product.

The source of sheepmeat for processed foods is usually from older sheep, typically mutton,[174] which is a cheaper source than lamb. In these processed foods the meat is usually comminuted,[175] which eliminates any problem of toughness due to muscle origin and animal age. However, mutton is more strongly flavored and, due to the negative perception by some consumers, its inclusion into meat products is never routinely promoted; for exammple, mainstream sausages prepared with mutton are often labeled "beef-flavored sausages" to avoid consumer misapprehension. Conversely, this is why "mutton-flavored sausages" are never seen.

The aversion of some consumers to meat taken from older sheep was investigated in New Zealand research by Lim,[176] who conducted a survey at a major agricultural show with 400 respondents. The female to male ratio was 1.6:1, with a wide spread of ages. Most respondents were of European descent. With no meat consumed or on view, they were asked to score seven meats for how good was their taste, their quality, and their healthiness (Figure 4). Only the first of these attributes has an objective base, but all respondents scored the three attributes without comment. The left-to-right sequence of species on the ballot had lamb, hogget, and mutton well spaced,

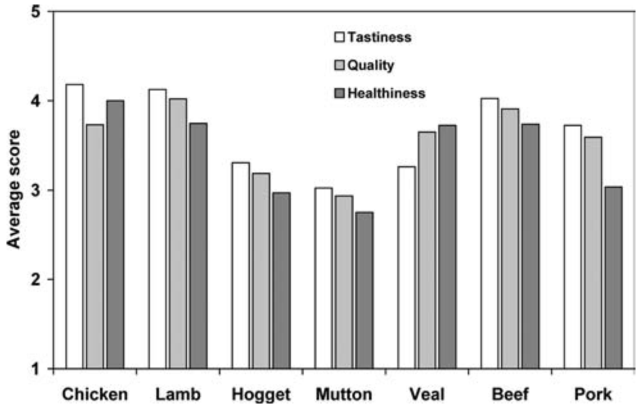

Figure 4. Consumer perceptions of meat attributes; 1 is low and 5, high. Data are means for 400 consumers. Standard deviation bars have been deleted for clarity, but very many of the differences were highly significant.

but is presented in Figure 4 for easy comparison of lamb, hogget, and mutton results.

Means for lamb and beef were similar, but the perceptions of hogget and mutton attributes were strikingly lower. The perception for mutton taste may be based on reality and for mutton quality may have its origins in tenderness, but with hogget the name is probably the driver of perception. This is because the objective eating quality attributes of sheepmeat are closely similar for lamb (roughly to age 1 year) and hogget (1–2 years).[29] Considering that at one point in a sheep's life a hogget is only a day older than a lamb, the name hogget has had an unfortunate marketing consequence. With the exception of a veal/beef distinction, no other meat type in Figure 4, or venison, is fraught by names based on age.

Looking beyond perceptions within a population, there is no doubt that populations around the world vary in their liking of sheepmeat. Sheepmeat consumption in Australasia is hundreds of time greater than in Japan,[1] and this is reflected in product habituation. Prescott et al.[177] spiked grain-finished beef with zero, low, and high concentrations of mixed BCFAs and of 3-methylindole to simulate nine flavor combinations of sheepmeat raised on pasture, representative of sheepmeat typically available to New Zealand consumers. These combinations were assessed as "minced meat" by female Japanese and New Zealand consumers. For the Japanese consumers, there was a strict linear decrease in liking as BCFA concentration increased. New Zealand consumers, by contrast, liked the low level of added BCFA concentration best, confirming the effect of habituation. The results for skatole were more complicated, but the highest concentration was clearly most disliked by both populations.

In contrast, had males been included in these trials, the results may well have been different. Young et al.[178] assessed liking of nitrite/salt-cured sheepmeat sausages to which sugars were added to reduce perceptions of sheepmeat flavor through the generation of Maillard reaction products that could mask the flavor. Xylose addition was the most useful, but of more interest was a gender effect on identification. The source meat was not identified and respondents had to identify the species from a proffered list of five. Misidentification was greatest with xylose, but much more so for males than for females. On the basis of some disparate research on perceptions of volatile FAs, it was proposed that misidentification may be associated with the likely greater sensitivity of females to these FAs, which are components of sweat.

The concept that females are more sensitive to volatile fatty acids, which include the branched-chain fatty acids of interest, has support in an unrelated study of goat yogurt.[178] Goat fats also contain the BCFAs that occur in sheep fats, which along with other (free) FAs can be rendered mostly nonvolatile by forming inclusion complexes with cyclodextrins added to liquids such as milk and yogurt. β-Cyclodextrin was much less effective with females than with males in masking "goaty" flavor in yogurt.

Given that unhabituated consumers are less accepting of sheepmeat, it remains a challenge to overcome the perceived negative connotations of the meat product, whether due to the inherent presence of a "natural" lamb flavor or due to the presence of BCFAs that contribute to the 'mutton' flavor. To overcome the barriers in these populations, masking lamb flavor with herbs and spices is an obvious path to take. Each culinary tradition has well-defined "flavor principles"[179] that could be utilized to produce an acceptable meat product suitable for unhabituated consumers. The importance of this concept and approach was confirmed by Prescott et al.,[180] who compared the reactions to lamb, labeled as such, of ethnic Chinese females in Singapore with those of New Zealand females of European descent. The lamb was flavored to characterize Chinese cuisine. Despite the fact that the Singaporeans ate much less lamb, their liking of lamb flavored with Chinese spices far exceeded the liking of the same product by New Zealanders.

Lu[181] extended the work of Prescott et al.[177] by spiking beef with high concentrations of branched-chain fatty acids and skatole (together called sheep flavor). This meat was used in a glucose-fermented sausage, with which she compared the effects of sheep flavor, nitrite curing, and spicing (rosemary plus garlic extracts) in eight possible combinations. As isolated treatments, neither curing nor spicing affected the marked difference in liking between sausage treatments with and without added sheep flavor (respondents did not like the sheep flavor). However, combined curing and flavoring almost entirely overrode the negative effect of added sheep flavor. Thus, ovine and pastoral flavors should be more acceptable to unhabituated consumers where fermented sausage flavored with "flavor principles" is simultaneously cured.

Given that intense sheepmeat flavors can be masked by a number of treatments, there is no fundamental impediment to creating a range of sheepmeat products designed for the unhabituated. For the habituated, those who accept or even seek the sheepy flavor, only one impediment remains in producing desirable products from lower cost sheepmeat. It is the names hogget and mutton.

In conclusion, considerable attention in the past has been given to the presence of 'mutton' and 'pastoral' flavors in cooked sheepmeat. This is understandable given the impact that these can have on consumer acceptance of the meat product. However, as noted in this review, the feeding system can also affect the overall flavor of the final cooked product. The use of forage rape (*Brassica*) as a finishing diet for sheep is such an example. Very little work has been published that describes the positive impact that the feed systems, or any other production factor for that matter, can have on sheepmeat flavor. Thus, it becomes difficult to generalize and make sweeping statements in relation to the feed system because of the wide range of impacts that it has on flavor of the final product, ranging from none to offensive and, in the case of condensed tannins, reducing pastoral flavor. Obviously, further work is required to elucidate the reasons for the diversity of impact on sheepmeat flavor from differing pasture feed systems.

Realistically, the overall relationship between the feed system and the total flavor is probably far more complex than has been, or could be, covered in this review. Flavor in a food product is a combination of both aroma and taste, and over the past 50 years substantial research effort has been directed to characterizing the aroma component of sheepmeat. The meta-analysis presented in this review indicates that there are 15 significant volatile compounds which contribute to lamb aroma. In comparison, considerably less is known of how taste contributes to sheepmeat flavor (and to the flavor of meat and related products in general) due to the lack of published research in this area. Particularly, very little is known about nonvolatile taste compounds in lamb meat and the role that these components play in the overall sheepmeat flavor. This represents an imbalance in the knowledge presently available, and further research is required to develop a more comprehensive view of the impact of feed systems on the taste compounds, which, combined with the knowledge of sheepmeat, will give a more complete picture of sheepmeat flavor.

Additionally, further consideration needs to be given to the effect the feed system has on other meat components. For example, research is needed to investigate the effects of IMF on volatile generation and its effect on in vivo temporal release and perception. Diet affects the fatty acid composition or protein oxidation, which may have consequences on the overall flavor once the meat is cooked. Also, as noted earlier, further studies are needed to determine the roles that compounds such as BCFAs have on the flavor of lean lamb meat. Obviously, there is still much that needs to be learned on the impact of diet and related feeding systems, as well as other production factors, on sheepmeat flavor.

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