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Effects of grass feeding systems on ruminant meat colour and flavour. A review

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Abstract — Grass feeding has been reported to affect several meat quality characteristics, in particular colour and flavour. In this paper we have reviewed some differences in meat colour and flavour between ruminants fed concentrates and animals allowed to graze pasture. The possible factors influencing the differences have been also examined. We have examined a total of 35 experiments which report the effect of pasture vs concentrate finishing systems on beef meat colour. Meat from cattle raised on pasture is reported to be darker than meat from animals raised on concentrates if measured by objective (P < 0.001) as well as subjective (P < 0.05) methods. Several factors, not a specific one are responsible for this difference, variations in ultimate-pH and in intramuscular fat content between animals finished at pasture and those finished on concentrates, seem to play a major role. Diet also affects meat flavour in both sheep and cattle but the components involved seem to be different. In sheep pastoral flavour is mostly determined by the branched-chain fatty acids and 3-methylindole (skatole). An important role seems to be played also by some products of oxidation of linolenic acid and its derivates. In cattle the role of skatole seems to be less important than sheep because of the lack of the branched-chain fatty acids. The pastoral flavour seems to be mostly determined by products of oxidation of linolenic acid and its derivates which derives substantially from grass.

Résumé — Effets d’une alimentation à base d’herbe sur la couleur et la flaveur de la viande de ruminants. L’alimentation à base d’herbe est souvent proposée comme un facteur pouvant influer sur la qualité de la viande et notamment ses caractéristiques de couleur et de flaveur. Dans cette revue bibliographique sont regroupées des différences de couleur et de flaveur observées entre viandes de bovins ou d’agneaux provenant d’animaux alimentés au pâturage ou avec des régimes concentrés (souvent à base de maïs) et les rares éléments d’explication. L’analyse de la couleur de la viande bovine repose sur 35 essais différents. La viande provenant des animaux qui pâturent est plus sombre, quelle que soit la méthode de mesure, objective (luminosité L* mesurée au photomètre P < 0.001) ou subjective (critère visuel P < 0.05). Parmi les principaux facteurs pouvant expliquer cette différence, se trouvent les variations du pH ultime et celles du gras intramusculaire. Le régime alimentaire affecte aussi la flaveur des viandes de bœuf et d’agneau, mais les facteurs impliqués semblent différer entre...
1. INTRODUCTION

Many factors influence ruminant meat quality and all of them can be divided for simplicity into two categories: factors directly linked with the animal (breed, age, sex, etc.) and factors external to the animal (diet, weather, slaughtering procedures, etc.) indicated by the generic expression “environmental”. Among the environmental factors, feeding plays an important role in the determination of quality. However, the specific effects of the dietary constituents on meat quality are not easy to evaluate. The feeding regime can have an influence on animal growth rate and it is difficult to establish if the meat characteristics are due to the dietary components for their intrinsic properties or if the diet has influenced growth rate and the body composition in animals [48]. Different carcass fatness could lead to differences in the rate of rigor development even if the carcasses are stored under the same conditions [59]. This could influence meat colour, tenderness, etc. In most of the experiments that study the effect of a diet on meat quality, the animals are slaughtered at different ages (same weight, but different growth rate) or at different weights (same age and again different growth rate). This problem is particularly evident when studies make comparison between production systems. Of course these experiments are useful because they investigate real production situations, however a correct interpretation of the data is more difficult: how is it possible to discriminate between the effects of the diet on animal growth rate (and indirectly on carcass and meat quality) and the direct effects of the dietary constituents on meat quality? Another problem of interpretation of data is when a comparison of diets on meat quality is made between animals allowed to move freely and animals restricted in feedlots. The effect of feeding may be confounded with the different physical activity.

The principal characteristic of herbivores and ruminants in particular, is the capability of the micro-organisms present in their gut (or fore-stomach) to degrade (and utilise) the cellulose. Ruminants convert forages into products of high biological value, useful for human nutrition (meat, milk, blood). In recent years, however, the genetic potential of the animals and the different zootechnical practises have changed the situation. A high-producing animal, has not the capacity to ingest the energy requirements for his high production, totally by forages and requires concentrate supplementation.

Animals raised on different production systems produce different concentrations of volatile fatty acids (VFA) in the rumen. The metabolism of propionate is very different from that of acetate and from the VFA have origin some different compounds responsible for specific meat flavours. Since propionate is the predominant glucogenic fatty acid, in contrast to acetate [11], the VFA metabolism also influences glycogen deposition which has an effect on meat ultimate pH and colour.

The objective of this work is to determine what is known to date on the effect of grass feeding systems on ruminant meat colour and flavour. In conducing this review,
we have tried to determine which effects were biased by animal growth rate and which effects are directly due to the dietary components.

2. COLOUR

Although colour is only slightly correlated with the eating characteristics of meat [46], it is very important for the consumer’s choice. Meat colour is measured subjectively or objectively. Subjective measures are generally taken in chillers by people accustomed to it. There are four main problems arising from this kind of measure: (1) the methods utilized sometimes differ from country to country; (2) there is a strong influence of the different lighting in chillers; (3) the subjective assessment is subject to bias; (4) often meat is not allowed to bloom. The objective measurements are generally taken using the CIE colour system [9]. The three fundamental colour coordinates are L*, a* and b*. L* is the lightness and is a measure of the light reflected (100 = all light reflected; 0 = all the light absorbed); a* (positive red, negative green) and b* (positive yellow, negative blue) are the other coordinates. When conducting experiments, appropriate blooming is important to allow sufficient oxygenation of meat [54] and to reduce the impact of rigor attainment temperature on meat colour. Young et al. [77] found that the temperature of rigor attainment has an influence on meat lightness (L*) soon after rigor during the first hour of blooming. When the meat was allowed to bloom for two hours or more, no effect of rigor attainment temperature on meat lightness was detected (rigor attainment temperature was studied at 9, 14 and 24 °C). In many countries, for commercial reasons, meat colour is measured or assessed in abattoirs during the first 24 h post mortem. However recent research [77] questions the validity of these kinds of measurement because the correlation between meat colour at the abattoir and meat colour days or weeks later under display is poor.

2.1. Effect of pasture vs. concentrate finishing on meat colour

To evaluate the effect of production system on meat colour we have examined the literature published between 1977 and 2000. We have found 35 experiments which report the effect of pasture (100%) vs. concentrate finishing systems on beef meat colour (longissimus muscle). Since the differences reported by most of the authors concerned meat lightness (for objective measurements) or brightness (for subjective measurements), we have restricted our attention to these aspects of meat colour. The pattern of instrumental lightness or visual brightness of cattle longissimus muscle after grazing at pasture or after being finished on concentrate is shown in Figure 1. For each experiment we have determined the difference in percentage of lightness or brightness between animals finished on pasture and those finished on concentrate. The effect is evident and it is clear that meat from animals finished on pasture is darker than meat from animals finished on concentrate. Animal finished for 150 days on pasture had a value of L* about 5% lower than animals finished on concentrate. Considering values of L* of about 45, this difference could be quantified between 2 and 2.25 units. This percentage was even higher when colour was measured subjectively: after 200 days on pasture meat is reported to be 10% less bright than meat from animal finished on concentrates. However, the linear regression between objective L* value and time on pasture was more significant ($P < 0.001$; $r^2 = 0.74$) than the linear regression between visual brightness and time on pasture ($P < 0.05$; $r^2 = 0.44$). The cause of this effect is extremely difficult to evaluate because more than one factor plays an important role. As an attempt to explain this pattern, we have examined different factors that could have contributed to influence meat colour in these experiments. Direct effects of the diet on meat colour are considered rare and dependent on a direct effect of the diet.
on muscle myoglobin [28, 53]. However myoglobin was seldom measured in the experiments that we have examined and, when measured, generally did not differ between pasture and concentrate animals.

Meat colour may be also influenced by factors such as carcass fatness, meat ultimate pH, animal age, carcass weight and intramuscular fat content. Considering that the production system could have an influence on all of these factors, we have tried, through the results of the literature consulted, to describe the relation between production system, these parameters and meat lightness ($L^*$). For each of these factors we have examined if the meat from animals finished on pasture or on concentrate correspond to different lightness and/or to different values of each factor. The results are presented in Figure 2a–2e.

### 2.1.1. Carcass fatness

Fattier carcasses allow the muscle a slower cooling rate in chill rooms and therefore rigor is attained at higher temperatures. A slower cooling rate corresponds to a faster pH decline and could be responsible for differences in meat colour [19, 77]. When we tried to evaluate if the effects of animal finishing on meat lightness were biased by carcass fatness for the experiments that we have examined (Fig. 2a), the results seem to exclude this possibility. In several experiments we found indeed that even if carcasses from pasture were fattier than carcasses from concentrate, the meat was still darker. Therefore the effect of carcass fatness seems not to be extremely important for meat colour.

### 2.1.2. Ultimate pH

There is without doubt a high correlation between muscle ultimate pH and meat colour and lightness in particular [10, 37, 38, 53]. The under-nutrition is a primary cause of high ultimate pH in meats [8] since animals do not have the possibility to accumulate sufficient glycogen reserve in their muscles but this is not a case of major concern for this review. Although pasture feeding is typically rich in fibre and poor in starch and the ratio acetate/propionate is therefore higher, pasture-finished animals have generally normal ultimate pH (although higher than concentrate-finished animals). In an experiment with Angus-cross steers finished in ryegrass/clover pasture or maize-based diets, Young et al. [74] reported however a higher ultimate-pH variability in animals raised on pasture and a significantly lower residual glycogen and glycolytic potential. Similar results have been reported by Vestergaard et al. [62]. It is concluded that pasture-finished animals have, in normal conditions, enough glycogen to lead to a normal ultimate-pH. However a lower glycolytic potential and a higher disposition to glycogen-depletion response to pre-slaughter handling [6] could be a risk factor for high ultimate pH. As confirmation of this, Immonen et al. [29] reported that high-energy diets protect cattle from potentially glycogen-depleting stressors. Animals raised and finished on pasture are not generally accustomed to the
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Vestergaard et al. [62] found that Freisian bull calves assigned to extensive production system grazing during the summer and housed with roughage-based diets during winter had a darker longissimus dorsi and semitendinosus muscles than calves tie-stalled and fed concentrate ad libitum. No significant differences in the supraspinatus muscle were found. These differences could also be justified by a difference in ultimate-pH which was slight, but significantly higher on the samples from animals raised on extensive system. Similar results were reported by Muir et al. [49] which compared meat from 3-year-old Angus steers finished on a high quality spring pasture (rye-grass/white clover/ subterranean clover) with animals finished on feedlot for different durations (grass- and grain-finished animals achieved similar live and carcass weights.

Human presence and handling, differing from stall-finished animals and this could have also some influence on the pre-slaughter glycogen depletion. Data in Figure 2b indicates that lightness value in pasture- and concentrate-finished animals seems to be highly influenced by ultimate pH in some experiments. However, it should be noted that concentrate-finished animals showed a lighter meat colour even when the ultimate pH was identical between groups as evidence that ultimate-pH is not the only factor influencing meat colour between pasture- and concentrate-animals. Unfortunately, ultimate pH is not always measured.

2.1.3. Physical activity

Some authors [49, 62] consider the animal physical activity as a possible factor affecting meat colour. Vestergaard et al. [62] found that Freisian bull calves assigned to extensive production system grazing during the summer and housed with roughage-based diets during winter had a darker longissimus dorsi and semitendinosus muscles than calves tie-stalled and fed concentrate ad libitum. No significant differences in the supraspinatus muscle were found. These differences could also be justified by a difference in ultimate-pH which was slight, but significantly higher on the samples from animals raised on extensive system. Similar results were reported by Muir et al. [49] which compared meat from 3-year-old Angus steers finished on a high quality spring pasture (rye-grass/white clover/ subterranean clover) with animals finished on feedlot for different durations (grass- and grain-finished animals achieved similar live and carcass weights.

Figure 2. Mean values of longissimus muscle lightness ($L^*$) and: (a) fat thickness, (b) ultimate pH, (c) animal’s age, (d) carcass weight, (e) intramuscular fat content in the consulted experiments for animals on pasture (■) or concentrate (○). Points linked by the same line are referred to the same experiment.
Meat from grain-finished steers was lighter (blooming 30 min air temperature) than pasture-finished animals. The authors concluded that the differences in meat colour were probably due to the physical activity of animals finished in pasture.

Differences in meat visual brightness between Angus steers fed at age 14 months for 111 days on pasture (improved annual Australian pasture) or on a grain diet in feedlot were also found by McIntyre and Ryan [41] despite similar body weight and daily gain. Animals from pasture had darker meat and higher ultimate pH.

2.1.4. Age at slaughtering and carcass weight

Bidner et al. [4] found that Angus-Hereford and Angus-Hereford-Brahman steers raised on pasture and slaughtered at 482 kg live weight had darker lean colour (visual assessment) and higher myoglobin content \((\text{longissimus dorsi})\) than steers raised on feedlot. No differences in meat ultimate-pH were found between groups. However it is difficult to determine if there has been a specific effect of diet components on myoglobin content because the animals were slaughtered at different ages (31 months for forage-raised and 21 months for feedlot animals) and myoglobin is reported to increase with age with an impact on meat pigmentation [52]. However as reported in Figure 2c, pasture-finishing systems resulted in darker meat even in several experiments in which animals were slaughtered at the same age. Unfortunately in most of the experiments in which animals were slaughtered at the same age, the weight of the carcasses was highly different between animals raised on different production systems. For this reason we have verified if carcass weight could have been another element of bias for meat lightness in these experiments. As reported in Figure 2d, in most (but not in all) experiments, concentrate-finished animals had higher weights and lighter meat colour. When the weights were comparable, differences in meat lightness were also detected in some experiments but not in others. These results underscore the need for more experiments in which pasture- and concentrate-finished ruminants are brought to similar body weight gain and are slaughtered at similar age and weights. From these results it seems that slaughter weight is also important in determining meat lightness from cattle finished on different production systems.

An effect of growth rate (and compensatory growth) on meat colour was reported by Allingham et al. [1]. Brahman cross steers of age nine months were allowed to graze for 257 days on an improved tropical pasture (Australia) in order to allow a constant body weight gain. Other animals were raised with low quality grain hay for 100 days (weight loss) and then realimented on high energy feedlot for 157 days. The final body weight was similar between groups but the authors found that samples of \textit{semitendinosus} muscle were lighter (higher L*; meat was allowed to bloom for 1 h at 4 °C) in grain-finished animals than pasture-uninterrupted ones. Ultimate-pH was not responsible for this colour difference because it was identical between groups. Different growth rate with similar age and body weight was also studied by Barker et al. [3] in Wagyu × Angus steers and heifers. The authors designed an experiment with two production systems: a linear (16 months on a grain-based diet) and a deferred (8 months on forage and 8 months on grain). The meat was darker (visual assessment) in the deferred group with a slight but significant higher fat thickness for linear animals. Dufrasne et al. [14] found that Belgian Blue bulls slaughtered at 560 kg of body weight had higher L* value in the \textit{longissimus thoracis} muscle when the animals were finished indoor (FI) on a concentrate diet compared to bulls allowed to graze for 140 days at a high stocking rate (eight bulls per ha; botanical composition: \textit{Lolium perenne}, \textit{Phleum pratense} and \textit{Trifolium repens}) and then finished indoors (HGFI). Animals
allowed to graze for 140 days in a medium stocking rate (6 animal per ha) and then finished indoor (MGFI) showed a meat L* comparable and between the other two groups (indoor and high stocking rate grazing). The comparability between the lightness of sample from animal raised on MGFI and animals finished indoors, seems to indicate that the difference between HGFI and FI samples is not due to the different physical activities. Another interesting aspect of this experiment was the results for carcass tissue proportion. The adipose tissue proportion was indeed comparable between HGFI and FI animals. No difference in meat colour due to different cooling rates was therefore expected. Also, the difference in meat colour was not due to the ultimate pH which was comparable between FI and HGFI samples and the authors found no differences in myoglobin content and justified the difference in meat colour by the presence of pigments such as carotenoids found in the grass.

2.1.5. Intramuscular fat

Intramuscular fat content could be also responsible for part of the differences in meat lightness found between animals raised in different production systems. Fat is lighter in colour than muscle and therefore its presence could contribute to an increased lightness value. Hedrick et al. [25] reported higher values of lightness for Hereford-Angus crossbred steers raised on concentrate compared to animal raised on pasture. Difference in intramuscular fat content were considered by the authors to be responsible for these meat colour differences although they did not measure intramuscular fat but marbling score. Data from Figure 2e indicate that if intramuscular fat has an influence on meat lightness, it is not the only reason for differences found between meats obtained from animal raised in different production systems. In conclusion, an extensive production system tends to produce a darker meat. For this difference, however, several factors more than a specific one, seem to play a role.

3. FLAVOUR/ODOUR

Generally red meat consumers consider the meat obtained from animals raised on pasture to be different from that obtained from animal raised on concentrates, especially in terms of flavours. Hilliam (1995), cited by Keane and Allen [30] (data from European Union) report that “there is a perception amongst consumers that meat from animals produced less intensively has a better taste”. On the contrary, in the US grass-finished beef is less acceptable for its flavour than grain-finished beef [39, 45, 67]. Bailey et al. [2] report the term “grass” to indicate meat from cattle raised on forage diets; other descriptor include “milky”, “fishy”, “rancid”. Similar descriptors have been used for sheep meat [31, 68]. Some flavour differences between beef from animals raised on concentrate or on pasture are reported in Figure 3. It is evident from the graph that the strongest flavour descriptors such as “Barnyard” or “Grassy” are more intense in the pasture-finished animals. When studying meat flavour it is important to distinguish between the analytical approach which tries to describe a product independently from its appreciation and the hedonic approach which is linked to the consumer’s preferences [12]. The consumer’s preference between different flavours is dependent on previous experience and culture [58, 68]. For example, the flavour differences found between animals raised in different production systems have an effect on acceptability of US consumer’s [68]. We have found 16 experiments published from United States in which meat from cattle raised in pasture or concentrates was compared for the acceptability of its flavour. Only on two occasions flavour was considered more acceptable when the meat was from animals raised on pasture, while the meat from animals raised on concentrate was more
acceptable, especially after 100 or more days of treatment. It is likely that if similar tests were conducted in New Zealand or Europe, then different results would probably appear.

Some authors have tried to understand how long it takes for animals raised on pasture, to reduce the flavour characteristics of grass. Melton et al. [43] and Larick et al. [34] slaughtered some cattle out of pasture and others animals were instead switched to concentrate. At regular intervals some of these animals were then slaughtered. The results of flavour intensity are presented in Figure 4 and the data suggest that it takes at least 3 months to eliminate the typical grass flavours (milky and grassy).

Data relative to meat flavour between animals raised on different production systems, could be affected by different carcass fatness [44]. As discussed in the section regarding meat colour, production system could affect meat ultimate pH. Young et al. [78] report a reduction of sheep meat flavour and an intensification in off-flavours when meat ultimate pH is high. Similar results have been reported by Priolo et al. [51] when high ultimate-pH was caused by the presence of condensed tannins in the diet. Braggins [7] induced high ultimate pH in lamb meat by adrenaline injection. He found that meat at ultimate pH of 6.81 and even 6.26 had a more undesirable flavour as judged by panellists than meat at normal pH (5.66). In the headspace examinations the author identified 54 odour-active compounds. Ten of them (most of these compounds were aldehydes) were found to be pH-dependent. High-ultimate-pH beef meat has also been described as less acceptable by sensory panellists [13].

3.1. Compounds responsible for meat flavour and relationship with the diet

Over 1000 volatile compounds responsible for meat flavour have been identified
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in the action of enzymes involved in the synthesis of some BCFA between different ruminant species. Young et al. [75] found that male Romney lambs raised from 73 to 232 days of age on feedlots based on alfalfa (78%) or crushed maize (59%) had concentrations of BCFA significantly higher in the subcutaneous fat, compared to animals grazed on ryegrass/clover pasture for the duration of the trial. However the diet effect seems to be much less important than the sex effect (and age when linked to sexual maturity). For example, male rams (200 days of age) have been reported to have significantly higher amount of 4-methyloctanoic acid than castrated rams [60]. Also, in the experiment of Rousset-Akrim et al. [55] and Young et al. [70] 4-methyloctanoic and 4-methylnonanoic acids were higher in the male lambs slaughtered at around 215 days compared to animals slaughtered at 100 days or less. It is clear that an extensive feeding regime, at equal slaughter age, could result in a reduction of these methyl-BCFA in sheep because of the higher ratio of acetate/propionate due to the higher fibre content of forages compared with concentrates. It is not easy to understand the real relationship between increasing level of the BCFA and sheepmeat flavour and the interaction between BCFA and other compounds has been suggested [70].

3.1.1. Branched chain fatty acids

Between the compounds responsible for the typical sheepmeat flavour without doubt the methyl-branched-chain fatty acids (BCFA), and particularly 4-methyloctanoic and 4-methylnonanoic acids [47, 71] are very important. These compounds have been considered responsible for undesirable flavour of cooked mutton [63, 64]. Regarding their correlation with sheepmeat flavour/odour, Young et al. [70] showed that a high concentration of these acids corresponds with high sheepmeat odour; however sheepmeat odour could be very high even when their concentrations are not high. This means that other compounds are surely involved in the sheep meat odour/flavour. The dietary origin of the BCFA is clear: they derive from ruminal propionate. Ruminal propionate is the main source for liver gluconeogenesis [32]. However, when propionate levels exceed the capacity of the liver to metabolise it normally, there is production of BCFA [21]. The fact that sheep and goats, in comparison to cattle, accumulate these compounds as result of restricted-roughage high-grain diets, suggest a possible different mode and extent of propionate metabolism between ruminant species [61]. Ha and Lindsay [23] suggested a specific selectivity in the action of enzymes involved in the synthesis of some BCFA between different ruminant species. Young et al. [75] found that male Romney lambs raised from 73 to 232 days of age on feedlots based on alfalfa (78%) or crushed maize (59%) had concentrations of BCFA significantly higher in the subcutaneous fat, compared to animals grazed on ryegrass/clover pasture for the duration of the trial. However the diet effect seems to be much less important than the sex effect (and age when linked to sexual maturity). For example, male rams (200 days of age) have been reported to have significantly higher amount of 4-methyloctanoic acid than castrated rams [60]. Also, in the experiment of Rousset-Akrim et al. [55] and Young et al. [70] 4-methyloctanoic and 4-methylnonanoic acids were higher in the male lambs slaughtered at around 215 days compared to animals slaughtered at 100 days or less. It is clear that an extensive feeding regime, at equal slaughter age, could result in a reduction of these methyl-BCFA in sheep because of the higher ratio of acetate/propionate due to the higher fibre content of forages compared with concentrates. It is not easy to understand the real relationship between increasing level of the BCFA and sheepmeat flavour and the interaction between BCFA and other compounds has been suggested [70].

3.1.2. Indoles and phenoles

Sheep

Although BCFA contribute to the characteristic sheepmeat flavour, it seems that this is strongly correlated with the contemporay presence of 3-methylindole (skatole, a fecal-smelly compound) [70]. BCFA could be responsible for sheepmeat flavour and skatole could increase their perception. Because a more extensive production system reduces the concentration of BCFA but significantly increases skatole, it seems reasonable to conclude that pasture systems seem to increase sheepmeat flavour perception (the BCFA are at lower level but
still sufficient to “activate” sheep meat flavour). In an experiment with Romney lambs slaughtered at 132 and 232 days of age after grazing on ryegrass/clover or receiving concentrate on feedlot, Young et al. [75] and Young and Priolo [76] found that skatole was present in pasture animals but only at basal levels in concentrate animals. Sheepmeat odour and flavour perception of panellists was higher for pasture-raised lambs although BCFA, as expected, were higher in feedlot animals. In a principal components analysis between frequency of panel descriptions and chemical compounds, Young et al. [68], found skatole to be in the same quadrant of sheep meat perception (Fig. 5) and in the opposite quadrant of lamb perception. The panellists were New Zealanders, accustomed to eating ovine meat. In New Zealand the term “lamb” has a good connotation while “sheep” does not. The word “sheepy” is roughly synonymous with “mutton”, a decidedly negative term. A difference in the animals diet was therefore identified by panellist rather as a difference in the age of animals. This could be justified by the amplification of the BCFA perception caused by the skatole.

Skatole is a product of degradation of tryptophan and has been associated with unpleasant odour in meat from entire male pigs [5]. Why the level of skatole is higher in fat from ruminants finished on pasture is not clear. Young et al. [72] suggest that the higher ratio of protein/non-fibrous carbohydrate characteristic of grass diets, enhances skatole production through a higher deamination of protein amino acids by rumen microbes. It should be also noted that the diet has an important effect on the microorganisms species present in the ruminal liquor [61] and that different microorganisms may degrade tryptophan differently and therefore produce skatole.

**Beef**

The contribution of skatole to the typical pastoral flavour in beef seems to be less important than in sheep. In a recent study, Young et al. [68] showed that cattle switched from ryegrass/clover pasture to maize silage diets reduced the indole and skatole to basal concentrations in the kidney fat within two weeks (Fig. 6). However, when the rendered fat was presented to panellists for odour assessment, differences were found only for “milky” odour which was higher in pasture samples (Fig. 7). It is also interesting to note that the term “faecal” was avoided by

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**Figure 5.** Principal components analysis of correlations between frequency of panel descriptors and relative concentrations of compounds in sheep fat (from Young et al. [68]).
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3.1.3. Linolenic acid and its products of oxidation

The fatty acid composition of meat can also affect meat flavour [15]. Ruminal micro-organisms hydrogenate dietary lipids which results in an increase in saturated fatty acids in animal tissues compared to the diet profile. However, part of the unsaturated...
fatty acids could escape ruminal hydrogenation [22, 65] and diet can influence fatty acid composition of ruminant tissue [57]. Diets rich in concentrates normally increase the levels of unsaturation of fatty acids in ruminant fat [18, 31] and as a consequence fat appears to be softer [72]. This happens because the micro-organisms dominant in the ruminal environment when concentrate diets are given, perform a reduced hydrogenation compared to the micro-organisms dominant when the diets are rich in cellulose [66]. The unsaturated linolenic acid (C\textsubscript{18:3}) is a fatty acid characteristic of forage lipids [65] and is notoriously not synthesized by mammals [22]. Since part of the dietary linolenic acid escapes ruminal hydrogenation, animals raised on pasture have a higher proportion of this acid in the carcass compared to grain-raised ruminants [36]. In Hereford and Angus steers fed corn after grazing on pasture, Melton et al. [43], noted a reduction of linolenic acid concentration (from 2.16% to 0.86%) up to 140 days. Similar results are reported by Mandell et al. [39] in Limousin-cross steers and by Garcia and Casal [20] in Angus steers. Similar results have also been reported in sheep [56]. Grass diets, as important source of linolenic acid, lead to increased levels of long chain n-3 fatty acids synthesised from C\textsubscript{18:3} [66]. Two derivates of linolenic acid, the eicosapentaenoic acid (EPA; 20:5) and docosahexaenoic acid (DHA; 22:6) are restricted to the phospholipid fraction and probably play an important role in meat flavour formation during cooking [15, 16]. Very important implications for human nutrition have been described by Enser et al. [17, 18] and increased consumption of these fatty acids has been recommended. The variation of linolenic acid in intramuscular fat of cattle after grazing on pasture or fed on concentrate is reported in Figure 8 (based on results from 22 experiments). Grazing for six months on pasture has an effect of increasing intramuscular linolenic acid by 50% in cattle. Further time spent on pasture seems not to have an effect on linolenic acid proportion.

There are important flavour implications with this pattern because products of oxidation of linolenic acid have been associated with species flavours of meat as result of the formation of volatile compounds during cooking [40]. The oxidative degradation of fatty acids with the formation of an alkyl radical from a fatty acid occur faster with polyunsaturated fatty acids (PUFA) than oleic or linoleic acid [16]. Derivates of linolenic acid such as EPA and DHA are particularly prone to autoxidation. Meat derived from ruminants consuming grass is on the other hand, protected from oxidation by the presence of antioxidants in the grass [65]. For example, tocopherol concentration is much higher in green leaf tissue than in grain or hay [11] and this could have implications in both meat flavour and colour. Melton et al. [43] found that C\textsubscript{18:3} was positively correlated (P < 0.001) with milky-oily aroma and flavour and with sour flavour. Oleic acid (C\textsubscript{18:1}, characteristic of maize-based diets) was negatively correlated with these attributes. Melton et al. [42] found that higher levels of C\textsubscript{18:3} were related to less desirable beef flavour to untrained American assessors. Flavour intensity was
positively correlated with C$_{18:3}$ in a study that compared British and Spanish lambs [58]. Assuming that linolenic acid has a very important role in meat flavour, Young and Baumeister [69] proposed that one of the compounds responsible for pastoral odour in cattle is 4-heptenal, a product of oxidation of linolenic acid reported to be a highly unpleasant odorant. This compound was initially found in traces in sheep fat [69]. When was positively detected, in a principal components analysis of correlations between panel descriptors and compounds, 4-heptenal fell in the quadrant of unpleasant descriptors [68] (Fig. 5). Differences in 4-heptenal concentrations due to the diet were detected in the headspace of cooked longissimus muscle from lambs by Elmore et al. [16].

3.2. Effect of different type of pasture on meat flavour

Larick and Turner [35] found that meat from 17-month old Hereford-Angus heifers allowed to graze sorghum-sudangrass for 84 days had a sweeter flavour and a gamier aftertaste than meat from heifers allowed to graze on fescue-clover pasture. When the heifers were switched to feedlot (rolled corn, corn silage and soybean meal) the sweet flavour and the gamey aftertaste were significantly reduced after 54 days. As a possible explanation for the sweet flavour the authors considered the possibility that unsaturated lactones formed from the oxidation of C$_{18:3}$ could be contributing to the difference in sweet flavour. The same authors found that meat from heifers on fescue-clover had higher “sour” flavour than meat on sorghum-sudangrass. The passage from pasture to feedlot also significantly increased sour flavour. Seven different pasture species were utilised by Young et al. [73] to assess sheep meat flavour. Six-month old lambs were allowed to graze for six weeks single species swards of ryegrass (Lolium perenne), tall fescue (Festuca arundinacea), cocksfoot (Dactylis glomerata), Phalaris (Phalaris aquatics), Lucerne (Medicago sativa), chicory (Chicorium intybus) and prairie grass (Bromus wildenowii). Animals grazing on Phalaris gave meat samples with the highest intensity of foreign flavours and a higher ultimate-pH variability. However ultimate pH was not the only reason for the difference on meat flavour because even samples with normal ultimate pH gave high foreign flavours. An opposite result was reported by Park et al. [50] who found that meat from animals grazing lucerne had a higher incidence of foreign flavours than that of animals grazing phalaris. Anyway, except for the case of phalaris, the study of Young et al. [73] showed that meat from lambs fed seven different pastures did not differ in acceptability. In a comparison between lambs grazed on perennial pasture (Lolium perenne, Dactilis glomerata and Trifolium repens), Hopkins et al. [26] found that if the pasture was irrigated meat flavour was significantly reduced but no effect on meat acceptability was found. An increase of sheep meat flavour has been reported by Hopkins et al. [27] when Brassica napus was grazed in comparison with an irrigated pasture similar to that utilized by Hopkins et al. [26]. Meat acceptability was not compromised.

4. CONCLUSIONS

Diet components and particularly grass regimes can affect meat colour and flavour in both cattle and sheep. Meat from ruminants raised and finished on pasture is generally darker than meat from animals fed concentrates. This result has been reported by several researchers after measuring colour objectively as well as subjectively. It appears that more than one factor plays a role in these differences; the tendency to a higher ultimate pH, or the different growth rate between animals are two examples.

Meat flavour is also influenced by diet. In sheep, pastoral flavour seems to be determined by the association of BCFA and
3-methylindole (skatole). An important role also seems to be played by some products of oxidation of linoleic acid. In cattle, the role of skatole seems to be less important than sheep and pastoral flavour seems to be determined by products of oxidation of linoleic acid and its derivatives which derive substantially from grass feeding.

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REFERENCES

Grass feeding and meat colour and flavour


