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Review

Colour of bovine subcutaneous adipose tissue: A review of contributory factors, associations with carcass and meat quality and its potential utility in authentication of dietary history

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ABSTRACT

The colour of bovine subcutaneous (sc) adipose tissue (carcass fat) depends on the age, gender and breed of cattle. Diet is the most important extrinsic factor but its influence depends on the duration of feeding. Cattle produced under extensive grass-based production systems generally have carcass fat which is more yellow than their intensively-reared, concentrate-fed counterparts and this is caused by carotenoids from green forage. Although yellow carcass fat is negatively regarded in many countries, evidence suggests it may be associated with a healthier fatty acid profile and antioxidant content in beef, synonymous with grass feeding. Nonetheless, management strategies to reduce fat colour of grass-fed cattle are sought after. Current research suggests that yellow colour of this tissue is reduced if pasture-fed cattle are converted to a grain-based diet, which results in accretion of adipose tissue and dilution of carotenoids. Colour changes may depend on the initial yellow colour, the carotene and utilisable energy in the finishing diet, the duration of finishing, the amount of fat accumulated during finishing and the rate of utilisation of carotene from body fat. Differences in nutritional strategies which cause differences in fatty acid composition may be reflected by differences in fat colour and carotenoid concentration. Fat colour and carotenoids are prominent among a panoply of measurements which can aid the authentication of the dietary history and thus to some extent, the origin of beef, although this potential utility is complicated by the simultaneous rather than discrete use of forages and concentrates in real production systems.

Contents

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1. Introduction

The colour of bovine subcutaneous (sc) adipose tissue (carcass fat) is an important component of beef carcass quality (Wood & Fisher, 1997) and thus, beef carcass grading systems (Walker, Warner, & Winfield, 1990; Price, 1995; UNECE, 2004), in the United States, Canada, Australia and Japan. This is due to the variability of bovine carcass fat colour, allied to the consumer expectation of consistency in the colour of bovine fat, if present on retail cuts (Price, 1995). Crouse, Cross, and Seideman (1984) stated that in the United States, the colour of both lean and fat were becoming increasingly important in quality grading, a phenomenon that was a reflection of consumer tastes. In a recent survey of 900 individuals in Japan, Korea, Taiwan, Hong Kong and Mexico, it was reported that 80% of respondents favoured beef with white or light amber coloured fat (Anonymous, 2007). In most beef markets, excessive yellowness in bovine carcass fat colour is undesirable (Walker et al., 1990; Yang, Larsen, & Tume, 1992) and may incite a good deal of consumer purchase resistance, commensurate with a perception that yellow colour in this tissue necessarily indicates that an animal was in a diseased state at the time of slaughter (Anonymous, 1993). Negative perceptions of the quality of meat from carcasses with yellow fat also abound, with a widespread belief that carcasses with such fat necessarily come from older animals and hence, produce less tender meat (Anonymous, 1993).

Beef production systems represent the combined and interacting effects of genotype, gender, age at slaughter and nutrition before slaughter (Moloney, Mooney, Kerry, & Troy, 2001b). Since feed costs are a major component of total variable costs in beef production systems, the temperate maritime climate in much of North-Western Europe, Britain and Ireland, conducive to pasture production and utilisation (Lee, 1988) ensures that grazed and conserved grass is an important source of feed for ruminants, including cattle, as it represents a renewable and relatively cheap source of feed (O'Riordan and O'Kiely, 1996). Pasture-based beef production is also commonplace in countries such as New Zealand (West et al., 1997) , Australia (Lanari, Rablin, Brewster, Yang, & Tume, 2000), Mexico (Izaguirre & Miyasaka, 2001) and Argentina (Pensel et al., 2000; Gómez & Rosso, 2002). In contrast, in regions such as southern Europe, where permanent grasslands are subject to severe moisture stress (Lee, 1988), cattle production does not rely to such a large extent on grass as a source of feed (Gigli & Iacurto, 1995).

Cattle produced in such diverse situations exhibit contrasting carcass fat colour. Consumer perceptions of what constitutes a 'normal' carcass fat colour may reflect regional variation in beef production practices. Consumers in Mediterranean Europe perceive beef that has 'white' or 'pale' adipose tissue to be of superior quality (Anonymous, 1999), a perception that is replicated in beef markets of North-East Asia (Morris, Purchas, & Burnham, 1997; Barton & Pleasants, 1993), including Japan (Muramoto, Nakanishi, Shibata, & Aikawa, 2003) as well as the United States (Wood & Fisher, 1997).

However, yellow fat is positively associated with traditional, grass-based beef production (Wood & Fisher, 1997) and is perceived as a positive quality criterion which is more "ecologically favourable" and can influence consumer purchase decisions (Schwarz, Augustini, & Kirchgessner, 1997). Healthy cattle that are reared on pasture or which consume green leafy forage accumulate carotenoids in their adipose tissue which results in the tissue acquiring a yellow colour (Morgan & Everitt, 1969; Yang et al., 1992; Strachan, Yang, & Dillon, 1993). It is widely accepted that grass feeding can impart positive and beneficial effects on beef quality from a nutritional perspective, particularly in relation to the fatty acid profile (French et al., 2000b; Moloney et al., 2001b) and antioxidant content, with the latter also improving certain aspects of meat quality (Wood & Enser, 1997). In this regard, potential exists for using fat colour or carotenoid concentration as an indicator of dietary history from which inferences regarding nutritional and meat quality can be drawn and authentication of grass-feeding accomplished (Priolo, Prache, Micol, & Agabriel, 2002; Prache et al., 2002).

Management strategies to reduce carotenoid concentrations and thus yellow colour in bovine sc adipose tissue, in line with consumer expectations in certain markets, have employed use of grain-finishing of pasture-reared cattle (Forrest, 1981; Strachan et al., 1993; Morris et al., 1997). However, although several sources of variation in colour of bovine carcass fat are known, limited definitive information is available regarding the underlying mechanisms that control changes in this aspect of adipose tissue appearance and quality. Hence, this review aims to summarise current knowledge regarding (i) factors that affect bovine carcass fat colour, (ii) strategies to reduce yellow colour, (iii) associations between carcass fat colour and meat quality, to acknowledge the potential valuable role that carcass fat colour could play in authentication of beef.

2. Effects of production system and management practices on bovine fat colour

Beef production systems depend on climatological and socio-economic factors which frequently dictate management practices and decisions, and thus are a composite of combined and interacting factors that relate intrinsically to the biology of the bovine such as its breed, gender, age at slaughter and carcass weight and fatness as well as extrinsic nutritional and environmental factors. Many of these factors will be discussed individually in the present review.

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Several studies have been conducted to elucidate the relationship between the management strategies used to finish cattle and the colour of sc fat (Strachan et al., 1993; Forrest, 1981; Craig, Blumer, & Barrick, 1959). Where cattle have grazed intermittently or seasonally, the issue of the length of the finishing period required to reduce yellow colour in carcass fat is also important. Many other studies have focused on the broader issue of carcass and/or meat quality as it is affected by forage- or concentrate-based finishing diets (Muir, Smith, Wallace, Cruickshank, & Smith, 1998; Schaake et al., 1993; Bidner et al., 1986; Crouse et al., 1984; Harrison et al., 1978) but have included commentary on the differences in the fat colour. However, data available in the literature are equivocal in this regard. Several similar studies have concluded that there was no difference in the fat colour of forage- and concentrate-fed cattle (Mandell, Gullett, Buchanan-Smith, & Campbell, 1997; McCaughey & Cliplef, 1996; Bidner, Schupp, Montgomery, & Carpenter, 1981; Dinius & Cross, 1978; Young & Kauffman, 1978).

While grass-feeding is synonymous with yellow colour in beef carcass fat, it must be borne in mind that beef production is generally a mixture of strategic feeding of grass and cereal/concentrate with the balance of feed types depending on factors such as the age of the animal, the stage of production and availability of a particular feed, which can have a seasonal influence. Such details are provided by Keane and Drennan (1991). In grass-based systems in North Western Europe strategic supplementation with concentrates is usually carried out while feeding grass (or maize) silage during indoor overwintering or during the typical indoor finishing phase.

Thus, references to 'grass-based' or 'cereal-based' beef production are assumed to indicate which of these feed types constitutes the dominant part of the diet, especially in the months preceding slaughter. In many situations a pattern of feeding is established whereby, if cattle spend periods at pasture intermittently or seasonally, a 'beef production system' can generally be regarded or described as 'grass-based'. In such systems, the pattern of both carotenoid and energy intake may vary considerably.

In New Zealand, for example, the beef finishing industry relies heavily upon pasture feeding (Boom & Sheath, 1997). In North-Western Europe also, the temperate, maritime climate ensures that grass growth and grassland utilisation is a prominent feature of agricultural systems (Lee, 1988). In such situations, where climatic conditions tend to favour grass growth, efficiently managed grazed grass can be the cheapest feedstuff for ruminants (O'Riordan and O'Kiely, 1996; McGee, 2000). In Ireland as in New Zealand, the main source of feed for cattle is grazed grass and grass conserved as hay or silage (Drennan, Keane, & Dunne, 1995) and due to an annual deficit in cereal supply relative to demand cereals as well as agro-industrial by-products are imported from warmer climates for animal feedstuffs (O'Mara and Mulligan, 2000).

Since the majority of Irish calves are Spring-born and the most widely practised systems of animal management involve steers, finished from about two years of age (Moloney, Keane, Dunne, Mooney, & Troy, 2001a), with a grazing season lasting approximately from March to early November (Lynch, Kerry, Buckley, Morrissey, & Lopez-Bote, 2001), by the time of slaughter at 28 to 30 months (typically as steers) it would be usual for cattle to have spent two-thirds of their lifespan at pasture. Comparable periods are likely to be spent at pasture in other countries where grass-based beef production is commonplace such as New Zealand, Uruguay and Argentina.

Conservation of grass by ensilage is a necessary grassland management tool in North-Western Europe to balance the asynchrony between seasonal grass surpluses (during summer) and year-round feed requirements (to balance a deficit of supply during winter months). Grass silage is the dominant feedstuff offered to cattle in the winter months in Ireland, often accounting for up to 25% of total annual feed DM consumption (O'Kiely et al., 1993), although supplementation with concentrates is the usual practise when cattle are finishing indoors (Drennan et al., 1995; Moloney et al., 2001a). In comparison to countries such as Ireland and New Zealand, the situation is very much different in regions with a Mediterranean climate such as Southern Europe.

Although Mediterranean Europe covers a vast and diverse area, one common feature is that grasslands are usually subject to moisture stress (Lee, 1988). Taking Italy as an example, in the north pasture production is insufficient and it can only be utilised from May to September. Though subject to local variation, pasture can only be relied on to support beef production for a period of three to four months (Gigli & Iacurto, 1995). Consequently, production of animals does not rely solely on pasture. A concentrate supplement is usually required, either on an all year round basis where pasture production is insufficient to graze animals, or in periods of restricted pasture production (Gigli & Iacurto, 1995).

In Italy, cattle tend to be fattened in specialised centres housing between 200 and 500 animals with meat destined for large urban populations (Gigli & Iacurto, 1995; Boyazoglu, 1990). Cattle diets consist mainly of maize silage, maize meal, barley, beet pulp silage and protein supplementation and both male and female cattle are usually slaughtered between 10 and 20 months (Gigli & Iacurto, 1995); 75% of beef consumed in Italy comes from young bulls below 22 months of age at slaughter (Carnovale & Nicoli, 2000). Hence, when comparing systems of beef production in regions such as North-Western and Mediterranean Europe striking contrasts are provided in terms of both extrinsic factors, particularly diet, and factors intrinsic to the biology of the animal such as age at slaughter (although the potential importance of the breed composition of the herd should not be underestimated). These factors can contribute to an explanation as to why typical sc adipose tissue colour can exhibit regional and international variation caused by different production systems.

3. Intrinsic biological factors that affect bovine carcass fat colour

Fat colour in the bovine is influenced by many intrinsic factors which include breed, gender and age (Table 1). Moreover, differences exist between ruminant species such as cattle and sheep with respect to their ability to absorb and deposit carotenoids, with consequent effects on carcass fat colour. Goodwin (1954) categorised mammals on the basis of their ability to selectively absorb carotenoids. Group (a) mammals accumulate carotenes and xanthophylls in their adipose tissue without discrimination, e.g. man; group (b) mammals accumulate mainly carotenes, e.g. cattle and horses; and group (c) mammals accumulate neither carotenes nor xanthophylls, e.g. sheep and goats. In contrast to previous work, Crane and Clare (1975) reported only xanthophylls in ovine adipose tissue although it appeared yellow.

Walker et al. (1990) conducted a comprehensive study of variation in sc fat colour of beef carcasses. Both objective measurements (CIELAB (1976) '*b*' value) and subjective assessments were made. The objective measurement of the sc fat yellowness explained 46% of the variation in subjective fat colour scores. Both the subjective visual colour assessment and the objective instrumental measurement followed similar trends. As subjective fat colour scores increased, an indication that the sc fat was becoming more yellow, the mean '*b*' value increased, which was also indicative of a more yellow sc fat. Walker et al. (1990) also reported:

For British breeds, diet, age, gender and interactions between gender and age as well as between age and hot carcass weight had significant effects on the '*b*' value of the sc fat.

Grass-fed cattle and 'milk vealers' had sc fat which was more yellow than feedlot cattle.

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Table 1
Factors that may affect yellow colour of bovine subcutaneous adipose tissue and carotenoid concentrations

Intrinsic Factors	Extrinsic Factors
Breed[a]	Diet[efgh]
Genotype within breed[b]	Carotene content[i]
Gender[a]	Plane of nutrition[c]
Gender × Age[a]	Diet × duration of feeding[h]
Age × Hot carcass weight[a]	Supplementation with vitamins A and E[ij]
Carcass fatness[c]	Forage:concentrate ratio[k]
Plasma carotene concentration[d]	
Lactation	
Growth rate[c]	
Rumen environment[m]	

[a] Walker et al. (1990).
[b] Dunne, Keane, O'Mara, Monahan, and Moloney (2004b).
[c] Knight et al. (2001).
[d] Knight and Death (2000).
[e] French et al. (2000a).
[f] Varela et al. (2004).
[g] Walsh et al. (2007).
[h] Dunne et al. (2006).
[i] Knight et al. (1996b).
[j] Yang et al. (2002).
[k] Loughery, (2001).
[m] King et al. (1962).

Females had yellower sc fat than steers, irrespective of age.

Differences between females and steers were less marked when both aged.

Older cattle had fat which was more yellow. Shemeis, Liboriussen, Bech Andersen, and Abdallah (1994) reported that older cull cows had more yellow carcass fat ($P < 0.01$). Buchanan-Smith and Mandell (1994) observed no yellow sc fat when youthful animals, under 2 years of age, were fed a wide range of forage diets, including pasture.

Dairy breeds had sc fat which was more yellow than British or European beef breeds. In agreement with this observation, Kruk, Malau-Aduli, Pitchford, and Bottema (1998) discovered that pure Jersey cows had higher β-carotene concentrations in their sc adipose tissue than either Jersey × Limousin or pure Limousin cows and produced more yellow sc adipose tissue, assessed subjectively, as a result.

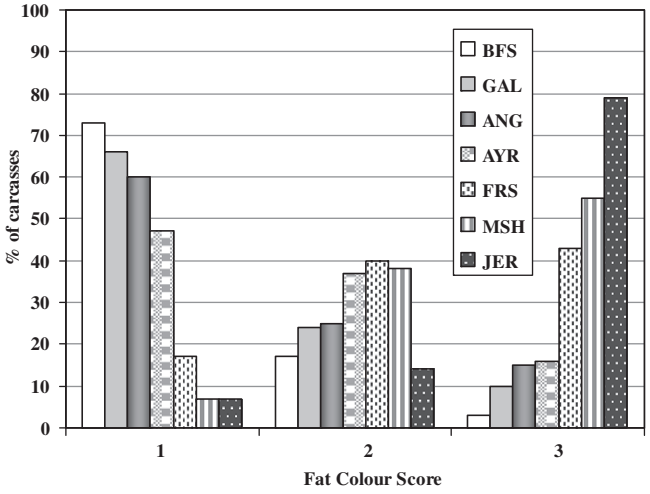

Fig. 1. Percentage of carcasses for each breed in each fat colour class after chilling. Colour assessed on a scale of 1 (very white) to 5 (very yellow), i.e. yellowness increases as fat colour score increases from 1 to 3. Breeds involved were Beef Shorthorn (BFS), Galloway (GAL), Angus (ANG), Ayrshire (AYR), Friesian (FRS), Milking Shorthorn (MSH) and Jersey (JER). Data from Barton and Pleasants (1993).

Barton and Pleasants (1993), who compared different breeds of steers raised on pasture and slaughtered at 30 months of age, found that beef breeds had significantly ($P < 0.01$) more carcasses with white fat than dairy breeds and the Jersey breed had more carcasses with yellow fat ($P < 0.05$) than any other breed (Fig. 1). Dunne, Keane, O'Mara, Monahan, and Moloney (2004b) reported that progeny of Friesians of New Zealand origin had carcass fat which was more yellow ($P < 0.05$) than Friesian progeny of Dutch/North American parentage or Belgian Blue × Holstein Friesian crosses, regardless of male status or slaughter weight.

4. Effect of diet on bovine fat colour

4.1. Carotenoids

4.1.1. Carotenoid chemistry, structure and physiological purpose in plants

Fresh and conserved pasture swards and other green forages contain chemical compounds called carotenoids that cause yellow colour to develop in the fat of bovines when such forages are eaten regularly. The main pigment responsible is β-carotene, and to a lesser extent lutein (Morgan & Everitt, 1968; Strachan et al., 1993).The carotenoids are a family of chemical compounds which possess a variety of distinctive yellow and orange colours. Chemically, they are classified as tetraterpenoids, with forty carbon atoms in their carbon skeleton. They are derived in nature from the metabolic intermediate, mevalonic acid, which provides the basic structural isoprene unit. The carotenoids comprise two distinct but related groups of chemical compounds, the carotenes and xanthophylls. The carotenes are strictly hydrocarbons while the xanthophylls, including lutein (3,3′ dihydroxy-α-carotene) are their oxygenated derivatives (Fig. 2). The carotenes occur in different isomeric forms, but *all-trans* β-carotene is the isomer most commonly found in forage crops. It occurs as several isomers, but these are usually not differentiated in the literature and are referred to interchangeably as carotene, carotenes or β-carotene (Kalac & McDonald, 1981).

Carotenoids are present in most photosynthetic organisms, including higher plants, although their presence is usually masked by chlorophyll. It is from this source that the bovine ultimately derives the carotenoids that are deposited in its adipose tissue since *de novo* synthesis of carotenoids does not occur in animals (Goodwin, 1992). In higher plants, these compounds are usually found as protein complexes in the thylakoid membranes of chloroplasts or in specialised sub-cellular organelles called chromoplasts. The principal carotene in most higher plants is β-carotene while the principal xanthophylls are lutein, violaxanthin and zeaxanthin. The carotenoids serve a dual physiological function in plants. They collect light energy that can be transferred to chlorophyll and used in photosynthesis and they protect chlorophyll from photodestruction during periods of excess light. Further details are available in Spurgeon and Porter (1980).

4.1.2. Chemical Analysis of Carotenoids

Historically, analysis of carotenoids in biological materials has involved saponification of lipids, ether extraction of the liberated, non-saponifiable carotenoids followed by spectrophotometric detection in the coloured extract, typically at wavelengths between 430 and 460nm (Kirton, Crane, Paterson, & Clare, 1975). A disadvantage with such methods was their inability to discriminate between carotenes and xanthophylls. In addition, the xanthophylls zeaxanthin and lutein are unstable with heating under alkaline conditions (Khachik, Beecher, Goli, & Lusby, 1992). Separation by thin-layer chromatography but more recently, high performance liquid chromatography has become the method of choice for sepa-

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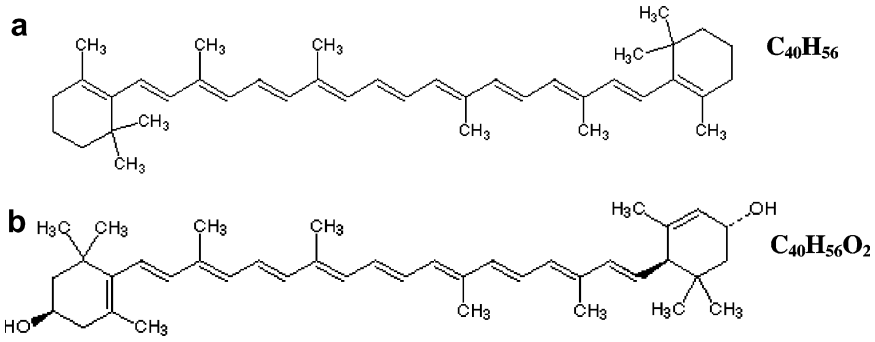

Fig. 2. Chemical structures of the carotenoids responsible for the yellow colour in bovine subcutaneous adipose tissue; (a) β-carotene; (b) 3,3' dihydroxy-α-carotene (lutein).

rating or isolating, identifying and quantitating extracted carotenoids in tissues and foods (Aust, Sies, Stahl, & Polidori, 2001; Khachik et al., 1992) and can be adapted for bovine adipose tissue and feedstuffs. Details of sampling and analysis procedures are provided by Brubacher, Muller-Mulot, and Southgate (1985) and Rodriguez-Amaya (1989) and some recommended chromatographic conditions are given by Aust et al. (2001) and by Khachik et al. (1992). Further details are provided by Nelis and De Leenheer, 1983, Lauren, Agnew, and McNaughton (1986), Lauren, McNaughton, and Agnew (1987); Singkamani, Koottathep, Supapang, and Thurnham (1989), Siong Tee and Lim (1991) and by Visser and Blair (1991).

4.1.3. Importance of beta-carotene/provitamin A in bovine nutrition

Carotenoids *per se* have not been regarded as essential in animal nutrition, although the principal carotene in higher plants, β-carotene, is important because it has pro-vitamin A activity. Historically, research on carotenoids has focused heavily on their activity as precursors of vitamin A, which was assumed to be their only function (Chew, 1993). Vitamin A plays a role in both the chemistry of vision and also in general health, including the formation and protection of epithelial tissues and mucous membranes. Deficiency symptoms may include night blindness, xerophthalmia, impaired appetite, retarded growth and infertility. Grazing cattle normally obtain an adequate level of vitamin A due to the abundance of carotene in grass relative to their requirements.

In more recent years, research on the broader implications of carotenoids for animal, and indeed human health, has gained more attention. As well as causing yellow colour in carcass fat, β-carotene is now accepted as a physiological antioxidant as well as a precursor of vitamin A (Lejeune, Peng, Le Boulengé, Larondelle, & Van Hove, 2000). According to Chew (1993), the activity of carotenoids as physiological antioxidants is probably independent of their activity as vitamin A precursors. The carotenoids can be classified among the antioxidant vitamins, together with vitamins E and C (Chew, 1996). β-carotene may also play a role in bovine fertility as it is found in the corpus luteum and follicular fluid (Buiter, 1998; Hurley & Doane, 1989).

4.1.4. Relationship between carotenoid content and colour of bovine fat

It has long been recognised that a relationship exists between the carotenoid concentration in sc adipose tissue and its yellow colour. Morgan and Everitt (1968) established a correlation co-efficient of 0.92 between the 'carotene' concentration and yellow colour intensity. Strachan et al. (1993) measured β-carotene and lutein concentrations in bovine sc and intermuscular fat. They found that the colour of both these fat depots, as assessed subjectively, was correlated with both β-carotene and lutein concentrations (for β-carotene r (correlation coefficient) = 0.55 and 0.61 for intermuscular and sc fat depots, respectively and for lutein $r = 0.52$ and 0.53 for intermuscular and sc fat depots, respectively). Dunne, O'Mara, Monahan, and Moloney (2006) reported that β-carotene and lutein concentrations separately explained 42% ($P < 0.001$) and 36% ($P < 0.001$) of the variation in s.c. adipose tissue yellowness, respectively, while total carotenoid concentration explained 46% ($P < 0.001$) of the variation.

Fat colour (subjectively assessed) was also correlated with β-carotene levels in the blood serum. Strachan et al. (1993) also measured the colour of intermuscular and sc fat using a Minolta chromameter (model CR200). The '*b*' values generated were also correlated with β-carotene and lutein concentrations in the intermuscular and sc fat (for β-carotene $r = 0.8$ and 0.85 for intermuscular and sc fat depots, respectively and for lutein $r = 0.73$ and 0.74 for intermuscular and sc fat depots, respectively). Zhou, Yang, and Tume (1993) reported a relationship between adipose tissue yellowness, measured using a Minolta chromameter (model CR200) and total carotenoid concentration in the tissue ($r = 0.79$; $P < 0.01$), with tissues containing carotenoid concentrations of 0.2 to 1.4 μg/g corresponding to '*b*' values of 6 to 18.

However, Swatland (1988) cautioned that the "subjective perception of grades of yellowness in bovine adipose tissue may involve something more than just their carotene content", which he speculated could have been residual quantities of oxyhaemoglobin. Irie (2001) reported that absorbance of deoxy- and met-haemoglobin (presumably from peripheral adipose tissue capillarisation) as well as carotenoids affected spectrophotometer absorbance, in addition to the reflectance, transmittance and fluorescence of lipids and the reflectance and fluorescence of connective tissue and cell membranes.

4.2. Carotenoid content of feedstuffs used in bovine rations

4.2.1. Forages

Forage refers to the vegetative portions of plants (Lee, 1988; Ellis, Wylie, & Matis, 1988) and includes natural and artificial or sown grassland (pastures), rough grazing, silage, hay, straw and annual and perennial green fodder from arable land (Lee, 1988). The β-carotene and lutein contents of a number of forages are summarised in Table 2. A number of factors influence the carotene content of forages. These include species and cultivar, stage of growth, fertiliser treatments, application of certain pesticides and the intensity of solar radiation (Kalac & McDonald, 1981). The carotene in forage plants is generally most abundant in fresh pasture since following harvesting and conservation, its concentration decreases (Bernstein & Thompson, 1947; Walsh & Hauge, 1953; Nehring & Hoffmann, 1967). Hay is a relatively poor source of carotene. Many factors impact upon this, including overmaturity and a higher degree of lignification of the grass when cut, weathering, heating and long storage (Bauernfeind, Adams, & Marusick, 1981).

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Table 2
β-carotene and lutein content of forages, cereals and root crops used in cattle diets

Feed	β-carotene (mg/kgDM)	Lutein (mg/kgDM)
Forages		
Fresh green legumes and grasses, immature (wet basis)	33–88[a]; 200–700[b]; 136–384[c]; 294–384[d]; 409, 134[e]	806, 356[e]
Legume silage (wet basis)	11–44[a]	NR
Maize and sorghum silages, medium to good green colour (wet basis)	4 – 22[a]; 9.1–18[f]	NR
Whole crop wheat silages, with/without urea application	NR	NR
Non-legume hays, including timothy, cereal and prairie hays, well-cured, good green colour	20–31[a]	NR
Non-legume hays, average quality, bleached, some green colour	9–18[a]	NR
Legume hays, including alfalfa, very quickly cured with minimum sun exposure, bright green, leafy	77–88[a]	NR
Cereals		
Barley	11–63.5[g], 10–12[h]	6–10[h]
Wheat	4- 9[ij]	NR
Root Crops/Miscellaneous		
Peas	3[k]	NR
Potatoes	Trace[k]	NR
Turnip	0.2[k]	NR
Carrot	125[k]	NR
Curly kale	32[k]	NR

NR: not reported.
[a] Adapted from McDowell (2000), reported as mg carotene/kg.
[b] Coultate (1996).
[c] Bauernfeind et al. (1981), perennial ryegrass *Lolium perenne*.
[d] Bauernfeind et al. (1981), white clover, *Trifolium repens*.
[e] Knight et al. (1996b), values for November, December.
[f] Nehring and Hoffmann (1967).
[g] Alvarez, Martín, and Martín (1999).
[h] Knight et al. (1996b).
[i] Kumar, Kaswan, and Madan (1995) and Mahal et al. (1998).
[j] Kumar et al. (1995) and Mahal et al. (1998).
[k] Food Standards Agency (2002), results are mean values and are given as mg carotene/kg.

β-carotene losses also occur during silage-making and subsequent storage (Nehring & Hoffmann, 1967). Most fresh green leafy material will contain between 200 and 700 mg carotene/kg dry matter (DM) (Coultate, 1996). Destruction of carotene occurs during ensilage, which is thought to occur due to the action of plant enzymes, including lipoxygenase (Kalac & McDonald, 1981). Lipoxygenase oxidises unsaturated fatty acids and other lipids containing a *cis-cis*-penta-1,4-diene unit, e.g. α-linoleic acid, and the resulting hydroperoxide radicals oxidise the carotenoids and other oxy-labile compounds (Kalac & McDonald, 1981).

Although grass silage is the most widely used conserved forage in northern Europe, the use of maize silage has increased in this region as plant breeders have developed maize capable of withstanding regional climatic conditions (O'Mara et al., 1998). Utilisation of winter wheat for silage production is popular in northern Europe as the crop can be grown in a wide variety of climates and soil conditions (Hill & Leaver, 2002). To reduce deterioration during storage, urea can be applied prior to ensiling to create alkaline silo conditions via bacterial hydrolysis of urea to ammonia (Hill & Leaver, 2002). However, there are no reports in the literature on the carotene content of this feedstuff.

Losses of carotene during ensilage are very variable, although usually low in well-preserved silages (McDonald, Henderson, & eron, 1991). Some 10% can be destroyed during the actual fermenting process, but losses of up to 30% have been recorded (Washburn, Krauss, & Monroe, 1947). The carotene content of silage depends on (a) carotene content of the original material; (b) possible losses resulting from intense feed fertilisation practices; (c) losses that occur during filling of the silo; (d) losses due to wilting; (e) losses during the fermentation period, and (f) storage losses (Bauernfeind et al., 1981). Kalac (1983) found that losses were highly variable and concluded that there was no clear relationship between silage quality and losses of β-carotene.

The carotenoid content is also subject to seasonal variation. Lipids in forages are generally positively related to crude protein and ether extract and negatively related to cell wall content (Nozière et al., 2006). Forrest (1981) reported that β-carotene levels reached a maximum value during mid-season, with levels dropping in both the Spring and Autumn, a trend that was repeated for xanthophylls. Forrest (1981) also reported that the xanthophyll content of the grass exceeded the carotene content approximately tenfold.

4.2.2. Concentrate feedstuffs

The feeding of concentrate feedstuffs, so called because they generally represent a more concentrated source of energy and protein than forage, tends to coincide with accommodation of beef cattle in an indoor environment in Europe and may be used to support a ration based on grass silage. Concentrates are usually either wholegrain cereals or formulated concentrates containing specified proportions of individual ingredients, each having a specific nutritional role. One common feature of concentrate feedstuffs in general, whether coarse wholegrains or formulated rations is that they tend to have very low levels of carotenoids (Table 2) although reliable data for carotenoid contents in animal feeds are difficult to find, as indicated by Nozière et al. (2006).

Oxidation of carotenoids may occur in manufacture of concentrate rations, where production methods may involve exposure of components to elevated temperatures coupled with grinding, mixing with minerals, the addition of fat and pelleting. When feeds are pelleted, destruction of both vitamins E and A may occur if the diet does not contain sufficient antioxidants to prevent their oxidation under conditions of moisture and high temperature (McDowell et al., 1996). Since carotenoids are structurally similar to these compounds and chemically vulnerable on the same basis, they are likely to be affected in a similar manner.

4.3. Comparisons of Diets

Schwarz et al. (1997) compared fat colour, among other aspects of carcass quality, of Angus × Simmental and Angus heifers finished on three different diets. Relevant data are presented in Table 3. There was no effect of treatment (diet) on carcass weight. Genotype had no effect on carcass fat colour but the indoor finished heifers had the least yellow carcass fat and tended to produce the fattest carcasses. The effect of a 90-day finishing period on fat colour after two seasons at pasture was minimal. Kerth, Braden, Cox, Kerth, and Rankins (2007) reported that Angus-crossbred steers fed exclusively on ryegrass pasture for 178 (d) before slaughter had more yellow sc fat over both the strip loin and ribeye roll than steers fed a high concentrate diet or a ryegrass/concentrate combination; ryegrass steers had lighter and less fat carcasses though (Table 3). Cooke, Monahan, Brophy, and Boland (2004) reported that heifers fed a high concentrate diet had a lower ($P < 0.001$) fat '*b*' value than those fed a grass silage/maize silage/concentrate diet, either unmixed or as a total mixed ration.

Walsh et al. (2007) fed five contrasting diets to steers and found that carcass fat yellowness tended to decrease in the order grass silage > whole crop wheat silage > ad libitum concentrates > maize silage > alkalage (Fig. 3a). French et al. (2000a), examining differences between five different diets, which had no effect on carcass weight or fatness, reported that feeding of either 6 kg grass DM plus 5 kg concentrates, 12 kg grass DM plus 2.5 kg concentrate or

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Table 3
Effect of diet on carcass fat colour, including data on carcass weight and an index of carcass fatness

A	Treatment			
Variable	MS-CON	PAS-GS	PAS-GSC90	Significance
Carcass weight (kg)	296 ± 6.9	286 ± 11.0	289 ± 13.1	NS
Fat Class	3.7 ± 0.4a	2.8 ± 0.5b	3.3 ± 0.6ab	*
Carcass fat '*b*' value	5.6 ± 1.1b	13.6 ± 2.3a	11.0 ± 2.7a	*
B	Treatment			
Variable	GRAIN	RYG-GRAIN	RYG	
Hot carcass weight (kg)	330.7 ± 10.26b	348.2 ± 10.26a	227.6 ± 10.26b	***
Fat thickness (cm)	1.1 ± 0.03a	1.0 ± 0.03a	0.6 ± 0.03b	**
Strip loin fat b^* value	18.3 ± 0.53c	21.9 ± 0.56b	24.4 ± 0.53a	***
Ribeye roll fat b^* value	18.1 ± 0.60 b	21.5 ± 0.63a	23.3 ± 0.60 a	***

A, Treatments were: indoors, with maize silage available on an *ad libitum* basis together with 1 kg concentrate per day (MS-CON), at pasture for two seasons, with an interim winter feeding period during which cattle were offered, a mixture of grass silage, hay and straw (PAS-GS) or as PAS-GS but with a 90-day indoor finishing period, PAS-GSC90.
a,b: means within the same row assigned different superscripts differ significantly ($P < 0.05$).
Fat class assessed according to EU Carcass Classification Scheme for the Carcasses of Adult Bovine Animals where conformation classes E (best), U, R, O, P (worst) are assigned numerical values 5, 4, 3, 2 and 1, respectively. Fat Score classes 1(least fat), 2, 3, 4H, 4L and 5 (most fat) are assigned numerical values 1, 2, 3, 3.66, 4.33 and 5, respectively.
Data from Schwarz et al. (1997).
B, Treatments were: cattle were finished on a high concentrate diet alone (GRAIN), on ryegrass for 125d then on a high concentrate diet for 94d (RYG-GRAIN) or on ryegrass alone for 178d (RYG). Fat colour at two locations, over the strip loin and the ribeye roll, reported.
a,b: means within the same row assigned different superscripts differ significantly ($P < 0.05$).
Data from Kerth et al. (2007).
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

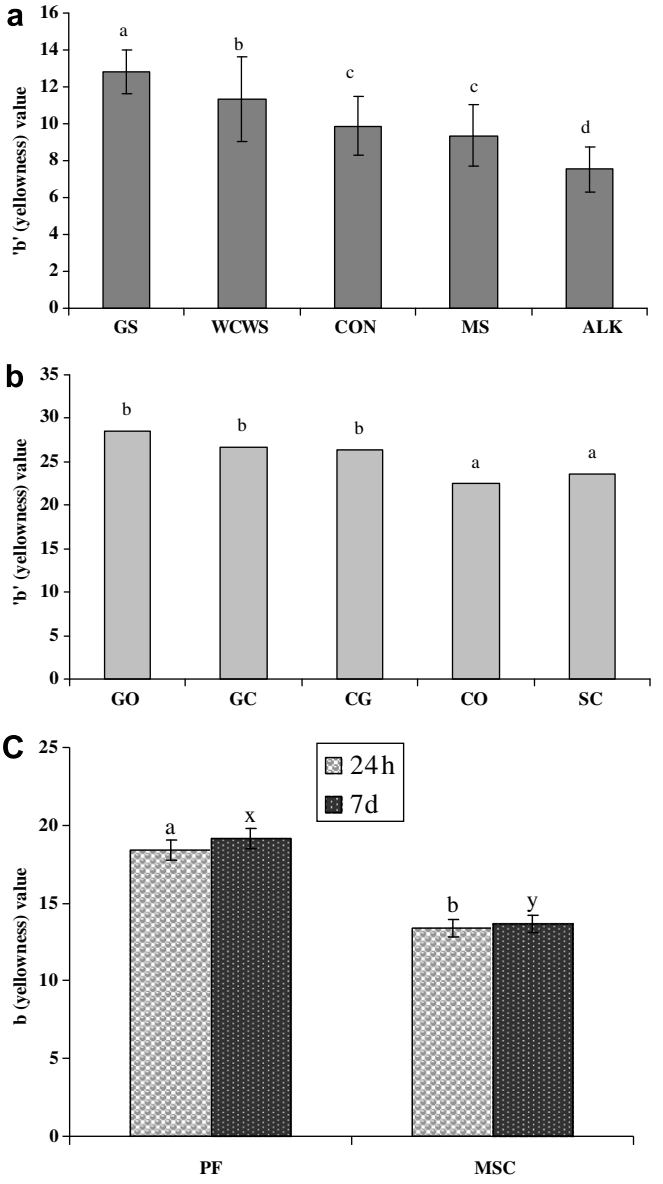

Fig. 3. Effect of diet on the 'b' (yellowness) value of bovine subcutaneous adipose tissue. (a)Mean values are represented for each diet; error bars represent the standard deviation of each mean. Diets offered were: GS, grass silage; WCWS, whole crop wheat silage, harvested at 400gDM/kg with no additive applied; CON, *ad libitum* concentrates; MS, maize silage; ALK, alkalage, i.e. wheat harvested at 700g DM/kg when golden in appearance, at 50%grain/50%straw, and treated with urea. (SED = 0.663; adapted from Walsh et al., 2007). (b) Mean values are represented for each diet. Diets with different superscripts differ significantly at P⩽0.05. Diets offered were: GO: 22kg grass dry matter (DM); GC: 12 kg grass DM plus 2.5 kg concentrates; CG: 6 kg grass DM plus 5 kg concentrates; CO: 8 kg concentrates plus 1 kg hay; SC: *ad libitum* grass silage plus 4 kg concentrates. Concentrate composition (g/100g) was ground barley (46), unmolassed sugar beet pulp (42), soyabean meal (8), tallow (1) and mineral/vitamin mix (3). (French et al., 2000a). (c) Mean values are represented for each diet; error bars represent the standard error of each mean. Diets offered were pasture-finishing for 3months (PF, $n = 16$) and finishing on a maize silage/concentrate diet (MSC, $n = 14$), also for 3 months. Carcass weights were 388.8 ± 13.25 and 387.8 ± 10.14 kg (mean ± SEM), for PF and MSC steers, respectively (adapted from Varela et al., 2004).

22 kg grass DM resulted in significantly more yellow carcass fat (Fig. 3b) as well as kidney fat in comparison with treatments not including grass, i.e. even moderate levels of grass inclusion caused more yellow fat. Varela et al. (2004) reported that steers finished on pasture had more yellow carcass fat than counterparts of equivalent carcass weight finished on maize silage plus concentrates, both at 24 h and 7 d post-mortem ($P < 0.01$ and $P < 0.05$, respectively) (Fig. 3c). French et al. (2000a) also reported that carcass fat yellowness (y) was inversely and linearly related to the proportion of concentrate in the diet (x) by the equation $y = -0.48x + 27.36$ ($r = 0.52$; $P < 0.01$) and that kidney fat yellowness (y) was similarly related to concentrate proportion ($r = -0.56x + 29.25$, $r = 0.69$; $P < 0.001$). Loughery (2001) reported a tendency for carcass fat yellowness and carotenoid concentration to increase linearly as grass silage intake increased from 12.5 to 25 and 37.5% of DM intake. Similarly, Dunne, O'Mara, Monahan, and Moloney (2006) reported that carcass fat '*b*' value was linearly ($P < 0.05$) related to the proportion of grass silage in the diet. Moreover, Dunne et al. (2006) reported that the effect of diet on fat colour depended on the duration of feeding; thus, although grass-fed heifers tended to have the most yellow fat when compared with silage- and concentrate-fed heifers, the differences between grass- and silage-fed heifers decreased over time. Yang, Brewster, Lanari, and Tume (2002) reported a ten-fold difference between mean β-carotene concentrations in fat of pasture- and grain-fed steers but did not report fat colour while Simonne, Green, and Bransby (1996) reported that feedlot finished steers had lower β-carotene concentrations in ribeye steaks than either pasture-finished steers or those finished on hay following withdrawal from pasture (Fig. 4a); they did not report fat colour. Richardson, Wood, Ball, Hallett, and Scollan (2007) reported that grass-fed steers had higher carotene concentration in sc fat (Fig. 4b) which was linearly related to CIE (1976) b^* value of the fat.

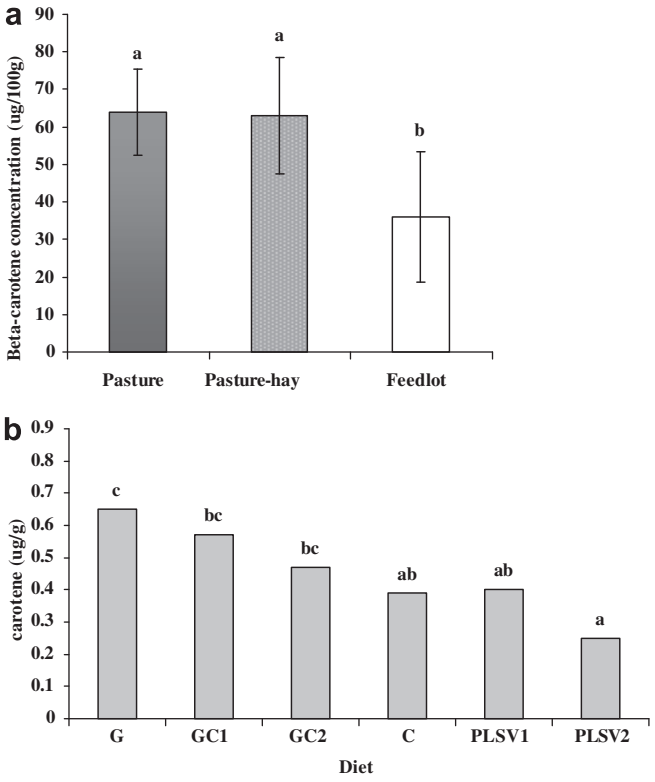

Fig. 4. (a) Effect of finishing diet on β-carotene concentration in ribeye steaks of steers. (Data from Simonne et al., 1996); (b) effect of diet on the carotene concentration in adipose tissue of Charolais steers. Diets offered were grazed grass (G); grazed grass plus 2.5 kg concentrates (GC1); grazed grass plus 5 kg concentrates (GC2); straw plus concentrate (C); straw plus concentrate plus ruminally protected lipid supplement with 25 mg/kg of vitamin E (PLSV1) and straw plus concentrate plus ruminally protected lipid supplement with 2000 IU vitamin E/day (PLSV2). (Data from Richardson et al., 2007). {Note: in a and b, y-axis scales are the same; 10 μg/100 g ≡ 0.1 μg/g}.

5. Influence of the rumen on the carotenoid content of bovine fat

5.1. Stability of carotenoids in the rumen

While reviewing carotenoids for ruminants, Nozière et al. (2006) commented that the extent of carotenoid degradation by microorganisms in the rumen remains uncertain because of the varying results, mostly with β-carotene, from both *in vivo* and *in vitro* studies and most likely attributable to the form in which carotenoids were delivered, whether in purified form or in forages. Several anomalous observations emerge from the study conducted by Yang et al. (1992). Firstly, cattle had the highest concentrations of carotenoids in fat yet they have the lowest concentrations in the rumen. Secondly, despite the fact that β-carotene is the dominant pigment in sc fat, accounting for approximately 80% of the carotenoid content, with lutein accounting for about 20%, β-carotene is present at levels of only around 7 to 9% of carotenoids in the rumen contents of cattle. Therefore, in going from the rumen to the fat depots a concentration effect on β-carotene is evident. Lutein is the major carotenoid present in the rumen (Yang et al., 1992). Implicit in the figures for β-carotene of levels of 7 to 9% in the rumen carotenoids, is the fact that lutein (or similar xanthophylls) represents about 90% of the carotenoid content therein. This concurs with the observation of Forrest (1981) who found that xanthophylls were present in the pasture that was used at ten times the levels of carotenes, although this was subject to seasonal variation.

Yang et al. (1992) found that carotenoids became more concentrated in the digesta as it moved from the rumen to faecal discharge, except in the small intestine, owing to the large influx of digestive juices which diluted the carotenoids. However, relative to sheep and goats, cattle had lower concentrations of carotenoids along their digestive tracts. Yang et al. (1992) speculated that this reflected either a lower total carotenoid intake or a higher rate of carotenoid destruction in the rumen of cattle. King, Lohman, and Smith (1962) studied rumeno-reticular losses of vitamin A and carotene. Destruction was observed when carotene and vitamin A were incubated *in vitro* in rumen fluid. Recovery of carotene from inoculated but non-incubated tubes averaged 97.5% but recovery of carotene from tubes incubated for 9 h averaged 65.5%. The antioxidants santoquin and tocopherol each reduced losses in a 10 h incubation.

In contrast to these findings, Yang et al. (2002) used the β-carotene concentration of abomasum contents to estimate the amount of β-carotene ingested by cattle, since it was assumed that β-carotene underwent very little degradation in the rumen. This assumption was based on the results of Leedle, Leedle, and Butine (1993) who found that α-tocopherol was not degraded in the rumen. It could be assumed, on that basis, that β-carotene would not be degraded either, since both are very similar compounds and would likely be degraded in the rumen by the same mechanism. However, Larsen, Yang, and Tume (1993) concluded that dietary sources of plant lipoxygenases had the potential to be an effective method for controlling the uptake of dietary carotenoids in certain ruminant species on the basis of *in vitro* studies with lipoxygenase preparations and carotenoid-containing rumen fluid.

5.2. Effect of feed type on ruminal stability of carotenoids

Keating, Hale, and Hubbert (1964) examined the *in vitro* effect of rumen liquor from steers fed high or low grain rations on the degradation of vitamin A and carotene. The losses of β-carotene in rumen liquor were small except for the addition of nitrite to rumen liquor obtained from animals on a low roughage ration. The findings concurred with those of previous workers (Olson, Nelson, & Emerick, 1963; Shorland, Weenink, Johns, & McDonald, 1957) who had found that carotenes were relatively stable in the rumen.

Olson et al. (1963) investigated the effect of nitrate and some of its reduction products on carotene stability and concluded that destruction of β-carotene in the rumen of animals that were fed nitrate-containing forages did not appear to present a problem of practical significance. However, they suggested that high levels of nitrates in ensiled forages may enhance losses of β-carotene considerably. They also found that nitrite, which is formed from nitrate in the rumen, caused little or no destruction in a neutral or alkaline medium, but that in an acid medium nitrate additions caused rapid β-carotene disappearance even at pH levels which were biologically feasible.

Other work is available which suggested that carotene was poorly utilised, i.e. converted to retinol equivalents, on high-concentrate rations (Esplin, Hale, Hubbert, & Taylor, 1963). These workers found that one or more of the four steers in each treatment had less total liver vitamin A at the completion of the trial than at the beginning. This was despite the fact that the carotene content of the rations was determined twice weekly and that carotene intakes were assumed to be large enough to meet the requirements of the animal for vitamin A and allow for liver storage of any excess. As well as storing vitamin A in their liver (Yang et al., 1992) bovines are also capable of storing relatively large quantities of β-carotene in their liver. Yang et al. (1992) reported a mean concentration of 7.01 μg β-carotene/g of liver in cattle which was significantly greater than the concentrations in the liver of sheep or goats. They also reported a mean β-carotene concentration in bovine sc fat of

0.81 μg/g. β-carotene was not detected in the sc fat of sheep or goats.

Knight, Wyeth, Ridland, and Death (1994) stated that according to Slyter (1976) changing from a forage-based diet to a grain-based diet increased lactobacilli numbers in the rumen and caused a concomitant decrease in protozoan numbers. This was a consequence of chronic or subclinical acidosis, which reduced rumen pH. This condition is quite common in cattle that have been introduced to feedlots and fed a grain-based concentrate ration (Owens, Secrist, Hill, & Gill, 1998; Britton & Stack, 1986). Knight et al. (1994) stated that the biochemical and physiological changes that occur during chronic acidosis could negatively affect β-carotene absorption and/or the binding of β-carotene to the high density lipoproteins that transport it in the blood serum (Yang et al., 1992). Furthermore, they stated that this could affect the post-slaughter fat colour.

6. Underlying mechanisms and factors affecting colour changes in bovine sc adipose tissue

Having considered the compounds that are responsible for colour in bovine sc adipose tissue, their basic chemistry, origins, and challenges that they may face in the pre-absorption environment of the rumen, a further discussion of actual and hypothetical mechanisms contributing to changes, especially reductions, in bovine sc adipose tissue colour could be reinforced by consideration of current knowledge regarding the nature of this tissue, the dynamic changes it undergoes as well as the nature of carotenoid absorption and transport to adipose tissue.

6.1. Adipose tissue

The adipose tissue depots of the carcass include the sc, perinepheric, intermuscular and intramuscular depots. The sc adipose tissue is commonly referred to by the term 'subcutaneous fat' although the tissue is not a homogeneous body of 'fat' or triacylglycerols, although they do constitute the dominant substance present. Yang et al. (1993) reported the lipid and moisture contents of sc adipose tissue from both live cattle and carcasses. The sc adipose tissue from biopsy samples ($n = 42$) contained 67.5 ± 1.41g lipid/100g and 28.8 ± 1.23g moisture/100g whereas carcass samples ($n = 16$) contained 84.9 ± 1.22g lipid/100g and 12.9g moisture/100g. Adipose tissue is cellular in structure, with the size of an adipose depot dependent on the individual size and number of adipocytes it contains (Leat, 1976). The cell membranes and connective tissue components of bovine sc adipose tissue can have a strong influence on the perceived whiteness of the tissue by virtue of their reflectance and fluorescence under certain lighting conditions (Irie, 2001).

6.1.1. Increase in carotenoid concentration during carcass chilling

Samples of adipose tissue taken immediately or soon after slaughter can be presumed to have similar composition to the tissue in the live animal but the samples taken by Yang et al. (1993) were taken at approximately 24 h post-mortem after chilling overnight at 4°C. Knight, Death, Boom, and Litherland (1998) reported that the carotenoid concentration and '*b*' value of sc adipose tissue increased ($P < 0.05$; $n = 118$) while the carcasses spent the first 24 h in the chiller after slaughter, a phenomenon also acknowledged by Priolo et al. (2002) in lamb carcasses. They reported that this was due to an apparent loss of moisture and resultant carcass shrinkage and not to the decrease in carcass temperature *per se*. This observation is corroborated by the findings of Yang et al. (1993) whereby lipid increased and moisture decreased (both $P < 0.001$) in carcass fat relative to sc adipose tissue in the live animal. The effect of moisture loss from a hot carcass would be to 'concentrate' the carotenoids in the carcass fat and hence, to cause increased yellow colour in sc adipose tissue, as seen by Knight et al. (1998).

Further evidence of such an effect is provided by Boom and Sheath (1997) who reported that carotenoid concentration (g/g) in the rump region of the carcass after 24 h in the chiller was higher than in the same area of the hot carcass, in both years of the study (1.34 ± 0.04 (hot) and 1.45 ± 0.05 (cold); 1.48 ± 0.035 (hot) and 1.59 ± 0.037 (cold)). However, Barton and Pleasants (1993) reported that chilling of carcasses for 24 h whitened the sc fat ($P < 0.01$) of all breeds that were studied, although carotenoid concentration was not determined and colour assessment was subjective.

6.2. Influences on carotenoid absorption

"All the mechanisms that control the absorption and assimilation of some carotenoids or that modify others during ingestion, are not fully understood" (Bauernfeind et al., 1981). Intestinal absorption and tissue distribution of carotenoids was reviewed by Parker (1996) and Furr and Clark (1997). Generally, the body fat of ruminants such as sheep and goats remains white regardless of their diet but cattle selectively absorb and deposit significant quantities of β-carotene and other carotenoids in their adipose tissues (Yang et al., 1992).

Despite its predominance in grazed pasture, Forrest (1981) failed to detect xanthophylls in the sc fat of steers. This led the author to speculate that either the steers had selectively absorbed the β-carotene, the minor constituent in the grass, or that they had degraded the xanthophylls by means of a hypothetical xanthophyll oxidase system. This was first proposed by Goodwin (1954) and was confirmed by Hill (1962) who was conducting an investigation into the occurrence of yellow fat in sheep.

The conversion of β-carotene to vitamin A occurs mainly in the intestinal wall by means of a hypothetical intestinal wall enzyme complex called the carotenase system. Zinc acts as a prosthetic group for alcohol dehydrogenase which participates in the conversion of β-carotene to vitamin A (Chhabra, Arora, & Kishan, 1980). The enzyme β-carotene-15,15'-dioxygenase cleaves β-carotene into retinal (Nagao, Maeda, Lim, Kobayashi, & Terao, 2000) although enzymes catalysing the asymmetric cleavage of β-carotene have been identified (Kiefer et al., 2001). However, the complexities of carotenoid metabolism in ruminants and their implications for fat colour and product quality require further investigation.

If greater quantities of β-carotene could be converted to vitamin A in the intestinal mucosal membrane of bovines this would reduce the amount available for absorption to the bloodstream. With this objective in mind, Knight, Death, and Wyeth (1996a) carried out three experiments to investigate the effect of supplementary zinc oxide (ZnO) on plasma carotenoid concentrations. In the first and second experiments there was no effect of drenching cattle with ZnO on plasma carotenoid concentrations. However, when the grazing cattle in the third experiment were fed daily with 1 kg barley containing 10g ZnO, the plasma carotenoid concentrations of the supplemented group had increased by 22% at d 28 relative to the control group (8.6 μg/ml compared with 7.1 μg/ml).

These findings were in contrast to previous work (Chhabra et al., 1980) and were unexpected, since supplementation with dietary zinc would be expected to increase conversion of β-carotene to vitamin A and to cause a decrease in plasma carotenoids as a consequence. However, Knight et al. (1996a) suggested that the zinc status of the grazing animals could have been critical to the actual unexpected outcome.

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A similar hypothetical enzyme system, the 'xanthophyll oxidase' system is thought to be responsible for the degradation of xanthophylls in sheep. Cattle have a less efficient xanthophyll oxidase system. Evidence of this was provided by Yang et al. (1992) who found the xanthophyll lutein in bovine serum, indicating that an overspill of lutein had occurred from the intestinal tract to the circulatory system. However, in this study lutein was only a minor component in the serum relative to β-carotene.

Knight, Death, Muir, Ridland, and Wyeth (1996b) also examined the effect of supplemental vitamin A (retinol) on plasma, liver and adipose tissue carotenoid concentrations and colour of sc adipose tissue. Early work (Deuel, Hallman, Johnston, & Mattson, 1942) had suggested that vitamin A supplementation increased the catabolism of absorbed carotenoids and on this basis Knight et al. (1996b) hypothesised that daily feeding of vitamin A should reduce the carotenoid concentration in fat and fat colour.

In experiment 1, thirteen two-year-old Angus × Friesian steers were grazed on pasture, and six were supplemented with 1×10^6 IU vitamin A for 83 d. The plasma carotenoid concentration of the supplemented steers was 4.2 to 6.4g/ml lower than the control steers. However, there was no difference in sc adipose tissue carotenoid concentrations or in subjective or instrumental measured colour.

Another experiment (Knight et al., 1996b) involved ninety 3-year-old Angus steers, 10 of which were slaughtered at the beginning of the experiment, 20 were grazed on pasture and the remaining steers were fed a diet of 70% barley and 30% pasture silage on a feedlot either without a vitamin A supplement or with a supplement of 1×10^6 or 0.5×10^6 IU vitamin A. While the plasma carotenoid concentration of the steers at pasture continued to increase, it decreased in all feedlot treatment groups. Colour ('*b*' value) and carotenoid concentrations of sc adipose tissue were similar for all the groups on the feedlot but lower ($P < 0.001$) than for steers on pasture. Thus, although vitamin A supplementation caused a decrease in plasma carotenoid concentration, it had no effect on sc adipose tissue colour or carotenoid concentration in either experiment.

Yang et al. (2002) confirmed an apparent interaction between β-carotene and α-tocopherol (the dominant isomeric form of vitamin E) with regard to absorption from the small intestine to the bloodstream. A factorial experiment was carried out comparing pasture and grain-fed cattle that were either given no additional vitamin E or supplemented at a level of 2500 IU/head/ d. At all four sampling points during the 132 d experimental period, mean plasma β-carotene concentrations were highest for the unsupplemented pasture-fed group relative to all other groups, including the supplemented pasture-fed group.

This suggested that the supplemental vitamin E was antagonistic to β-carotene absorption. This is plausible since both β-carotene and vitamin E are lipid soluble and are structurally quite similar. Both rely on incorporation into micelles for absorption and so compete for micellar sites (Yang et al., 2002). Alternatively, since both are carried in blood by lipoproteins, competition for absorption sites in these structures may also occur.

Absorption of β-carotene was shown to be greater when cattle were fed a diet rich in polyunsaturated fatty acids (PUFA) (Ashes, Burley, Sidhu, & Sleigh, 1984) and in this regard, diets exclusively or predominantly based on grass contain more PUFA/kg DM than diets based on concentrates (Moloney et al., 2001b). French et al. (2000b) showed that grass and grass silage contained combined quantities of linoleic (C18:2) and linolenic (C18:3) acid that amounted to 63.15 and 60.76g/100g of fatty acid methyl esters (FAME), respectively, whereas the concentrate used only contained a combined amount of both of over 18 g/100g FAME. Cattle that graze pasture and produce more yellow adipose tissue than grain-fed cattle would also be expected to have a higher intake of PUFA, unless these compounds had been specifically added to a concentrate ration.

6.3. Plasma carotenoids

Once carotenoids have entered the bloodstream they are transported in the plasma in solution in the lipid core of lipoproteins, especially the high-density lipoproteins (Knight, Death, Lambert, & McDougall, 2001). Knight et al. (1994) monitored the carotene concentrations in blood plasma of 6 Jersey and 6 Angus heifers. The heifers were removed from pasture and fed a pelleted ration in several consecutive phases, with 500 mg of carotene/kg fed for 27 d, 250 mg/kg fed for 21 d and 0 mg of carotene / kg fed for 70 d, respectively, after which the heifers were returned to pasture. Knight et al. (1994) stated that while the major stores of β-carotene in the body are known (blood serum, liver and adipose tissue) the 'dynamic rate of turnover' of β-carotene in these stores remain unknown.

When the heifers were taken off pasture and introduced to the feedpad the plasma carotene concentration decreased rapidly. This would have been expected if the heifers had been placed on a diet which contained little or no carotene. However, they were placed on a pelleted diet containing 500 mg added carotene/kg which supplied a comparable amount of carotene to the pasture forage diet. The large decrease in the plasma carotene concentrations at 29 d following introduction to the feedpad was thus unexpected and was attributed by Knight et al. (1994) to development of acidosis after introduction to the feedpad, which they postulated may have led to changes in carotene absorption or the ability of high density lipoproteins to bind absorbed carotenoids.

However, plasma carotenoid concentrations began to increase after decreasing to a minimum of 3.5 ± 1.8g/ml at 29 d after introduction to pellets. Concentrations stabilised after the change to the pellets containing 250 mg added carotene per kg but following the change to the pellets that contained no added carotene, plasma carotenoid concentrations decreased immediately and followed an exponential decline according to the equation:

$$\text{Plasma carotenoid concentration} = 3.61e^{-0.0278x} + 4.73e^{-0.1004x}$$

where x = d after changing to the pellets containing no added carotene/kg.

The results demonstrated that blood carotenoids respond very sensitively to changes in carotenoid intake. Knight et al. (1994) concluded that there were two pools of carotene, one which was depleted rapidly and another which was depleted more slowly. Blood plasma and liver carotenoid stores were proposed as the stores which were turned over rapidly and the carotenoids in adipose tissue were proposed to be mobilised more slowly.

Plasma carotenoids have frequently been measured in an attempt to estimate the flux of carotenoids between different tissues where they are known to be either transported or stored. It has been presumed that changes in plasma carotenoid concentrations will preceed changes in sc adipose tissue carotenoid concentrations since changes occur in plasma much more rapidly than in adipose tissue, as evidenced by Knight et al. (1994). In this regard, Knight et al. (1996b) speculated that the reason for a lack of an effect of vitamin A on sc adipose tissue carotenoid concentrations may have been that plasma carotenoids were above a minimum threshold concentration, which they proposed to be around 6 to 7 μg/ml. The conclusions of Knight et al. (1994) support the observations of Yang et al. (1993) who observed a rapid decrease in serum β-carotene concentrations after feedlot entry despite there being no change in carotene concentrations in sc fat, indicating that while serum levels were rapidly depleted, changes in levels of β-carotene in sc fat occurred more slowly.

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6.4. Effects of lipid metabolism and changes in carcass fatness

An increase in the size of an adipose tissue depot results from a combination of hyperplasia and hypertrophy although hyperplasia is complete at an earlier stage in the development of the animal (Leat, 1976). The formation of adipose tissue depots is the net result of synthesis and mobilisation of fatty acids, which are in a continual state of flux, with the composition of an adipose depot representing an equilibrium of synthesis, interconversion, deposition and mobilisation (Leat, 1976). However, doubt remains about whether carotenoids, once deposited in adipose tissue, remain indefinitely or if they can be mobilised to fulfil some physiological purpose. Currently, the weight of scientific evidence available suggests that when on a constant diet, changes in colour and carotenoid concentrations of sc adipose tissue are caused primarily, but not necessarily only by changes in the size of this tissue. Information concerning the rate of turnover of carotenoids in adipose tissue, if this proposed phenomenon occurs, is speculative.

Yang et al. (1993) concluded that whether changes in fat colour are due to the mobilisation and oxidation of carotenoids in fat depots, or to a 'dilution' effect as the animal fattens was unknown. However, cattle which are fed a grain-based concentrate ration in feedlots normally achieve more rapid growth than their pasture counterparts but also produce fatter carcasses (Bowling, Smith, Carpenter, Dutson, & Oliver, 1977; Bowling et al., 1978; Harrison et al., 1978; Young & Kauffman, 1978; Schroeder, Cramer, Bowling, & Cook, 1980; Aberle, Reeves, Judge, Hunsley, & Perry, 1981; Bidner et al., 1981, 1986; Muir et al., 1998).

6.4.1. Lactation

Anecdotal evidence suggests that cows, and older cows from the dairy herd in particular, have more yellow sc adipose tissue (Walker et al., 1990). Use of such anecdotal evidence may provide indications as to the importance of the effect of lipid metabolism on the colour of bovine carcass fat. One feature of lactation and resulting lactogenesis in ruminants is that lipid metabolism is altered whereby lipolysis increases and lipogenesis decreases in adipose tissue (Swanson, 1989). Assuming that carotenoids are supplied in the diet and assuming their ongoing accumulation throughout the life of the cow coupled with intermittent periods of lipid depletion coincident with lactations causing a 'concentration' of carotenoids, a plausible explanation for the yellow adipose tissue of old dairy cows can be envisaged.

6.4.2. Compensatory growth and growth pattern

A feature of grass-based beef production systems is that cattle exhibit compensatory growth when moving from Winter to Spring pasture (in situations where they have been outwintered on pasture). During periods of restriction of feed/energy intake, adipose tissue fat reserves may be mobilised, thus concentrating carotenoids (Boom & Sheath, 1997). Boom and Sheath (1997) observed an increase in sc fat carotenoid concentration during winter when feed restrictions were imposed and claimed that as long as growing cattle were permitted to reinstate fat reserves there would no lasting effects on carcass fat carotenoid content. Butler-Hogg, Wood, and Bines (1985), in a comparison of 20 cows, with four in each of five separate physiological states found that in comparison with other adipose tissue depots sc adipose tissue experienced the greatest proportional change with changing physiological state. Therefore, it would be expected that in periods of an energy deficit, fat reserves in sc adipose tissue would be most depleted.

Barker, Mies, Turner, Lunt, and Smith (1995) compared American Wagyu × Angus steers and heifers which were produced in two systems; one was termed 'linear' where animals were grown at a constant rate for the duration of the trial, (454 d) and the other was termed a 'deferred' system where animals were grown slowly over the first 224 d on feed (0.49 kg/d) allowing compensatory gain to occur over the remaining 230 d (1.04 kg/d in comparison with 0.78 kg/d for the 'linear' animals over the equivalent period). However, neither fat thickness nor colour was affected by production system although, carcasses produced by the 'linear' growth path were more acceptable in terms of fat colour when assessed subjectively according to the Japanese beef grading system (Barker et al., 1995).

6.4.3. Dilution versus mobilisation of carotenoids as an explanation for reduced carcass fat colour

The colour of fat that is produced on a beef carcass appears to be directly affected by the carotenoid and energy content of the feed offered as the finishing diet. The production of fatter carcasses from grain-fed feedlot cattle is generally manifested by larger amounts of fat deposition in the main fat depots, i.e. sc, intermuscular, internal and intramuscular fat (Harrison et al., 1978). Depth or thickness of sc adipose tissue has been used frequently as an indication of carcass fatness (Tables 4 and 5). Offering an equivalent quantity of feeds that may contrast in carotenoid and energy content, such as a predominantly grass diet and a barley-based concentrate, would be expected to influence fat colour in two regards. Firstly, the quantity of carotenoids supplied by the grass-based diet will greatly exceed that supplied by a cereal-based diet (section 3.2), although some variation would be expected in the latter, depending on the individual ingredients, including the cereal grain used, and the processing conditions, if relevant. Seasonal influences will affect the carotenoid (Forrest, 1981) and utilisable energy (Givens, Moss, & Adamson, 1993) content of grass/herbage diets. Secondly, as stated, grain-fed cattle generally accrete more adipose tissue than cattle of a similar age fed grass or forage and increased adipose tissue accretion is thought to 'dilute' carotenoids.

Knight et al. (2001) conducted an experiment in which forty, 17 to 18-month old steers were fed a ration of maize grain, maize silage and soybean meal containing 6 mg β-carotene/kg DM, and were slaughtered 0, 28, 42, and 70 d after starting on the ration. Significant decreases ($P < 0.001$) occurred in sc adipose tissue '*b*' value after 70 d but sc adipose tissue carotenoid concentration decreased ($P < 0.01$) after only 28 d (Table 5). Decreases in fat yellowness coincided with increases in fatness suggesting that carotenoids were diluted by accumulation of triacylglycerols in adipose tissue. A decrease in sc adipose tissue carotenoid concentration from 0.84 mg/g initially to 0.47 mg/g after 70 d (a reduction of 44%) coincided with an increase in fat depth from 6.9mm to 9.6mm, an increase of 39% so that although the strategy in this experiment was to examine changes in colour and carotenoid content of sc fat over time, the results also suggest that the reduction in colour was caused in part by increased fatness in conjunction with the low carotenoid content of the diet.

Knight et al. (2001) conducted a further experiment in which 3 groups ($n = 13$ per group) of 24 to 26-month-old steers, were fed a ration of maize grain and pasture silage, containing 33 mg β-carotene/kg DM. The ration was fed to steers for 63 d at 1 of 3 allowances with the aim of gaining weight rapidly, gaining weight slowly or losing weight with a fourth group of steers slaughtered at the outset. The growth rates of the steers were 1.72, 0.71, and −0.03 kg/head/day for those gaining weight rapidly, slowly and losing weight, respectively. Steers gaining weight rapidly tended to have heavier and fatter carcasses than other groups. The yellowness and carotenoid concentrations of sc fat of the steers gaining weight rapidly were significantly lower than the group slaughtered at the outset or those losing weight ($P < 0.05$). There was no difference between groups gaining weight rapidly and slowly in terms of carotenoid concentration although those growing slowly tended to have higher concentrations (1.57 v 1.17 mg/g; s.e. = 0.15).

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Table 4
Experiments which have included comparisons of subcutaneous adipose tissue colour of cattle fed on different diets for different periods

Reference	Comparison	Colour difference	Fat thickness	Colour Assessment (Subjective/ Instrumental/Analytical)
Dunne et al. (2006)	Permanently-housed (PH-CON) v grazing (PAS - 90d) + concentrates (PAS-CON), grass silage (GS) at 20% of dietary dry matter (DM) (PAS-GS20), 50% of dietary DM (PAS-GS50) or zero-grazed grass (PAS-GRA). All treatments (T) receiving supplementary concentrates to ensure similar growth rates. Heifers slaughtered at days (D) 28, 56, 91 and 120 after housing.	T × D interaction for 'b' value in subcutaneous fat. GS and PAS-CON ↓between housing and d28 but while GS ↑ to d120, significantly so for GS50, PAS-CON tended to↓ but were more yellow than PH-CON on all days.	Not measured. However, no significant difference between treatments or slaughter days for intramuscular lipid content.	Instrumental (Minolta CR300 chromameter)
Muir et al. (1998)	Exp. 1: Pasture v feedlot ration (30% pasture silage: 70% maize silage) Pasture steers (n = 10) slaughtered initially; at 6, 10 and 14 weeks, steers (n = 10) slaughtered from pasture and feedlot groups	No difference	Increased as length of feeding increased*** and grass thicker v grain**	Instrumental (Gardiner Spectrogard reflectance spectrophotometer) 'b' value 17.2, 15.6 and 14.6 for 6, 10 and 14 weeks pasture 16.9, 13.6 and 14.8 for 6, 10 and 14 weeks feedlot
Morris et al. (1997)	Pasture (PAST) v concentrate supplementation at pasture (CONC/ PAST) v concentrates + straw in feedlot (CONC/STR)	No difference	Not given	Subjective (scale:1-8) Instrumental (Minolta Chromameter II) 'b' value 16.34, 16.06 and 17.15 for PAST, CONC/PAST and CONC/STR, respectively
Mandell et al. (1997)	97% alfalfa silage (AS) (155 days) v 68% high moisture corn (HMC): 25%AS (122d)(AS/HMC) v HMC from d42 to slaughter (d92)	No difference	No difference	Subjective (scale: 1 = bright yellow; 5 = white) 3.92, 3.96 and 4 for AS, AS/ HMC and HMC, respectively
McCaughey and Cliplef (1996)	Pasture v 33d and 75d grain	No difference	Increased with length of finishing period**	Subjective (scale: 1 = white; 3 = yellow) 2.1, 2 and 2 for pasture, 33 and 75d grain, respectively
Strachan et al. (1993)	See Table 5.			
Schaake et al. (1993)	Pasture (Fescue-clover (FC); FC + summer pasture (FC+SP)) v 45, 75 or 170d drylot	Pasture more yellow*	Increased with length of drylot feeding*	Subjective (2 = slightly yellow; 3 = slightly white; 4 = white) 2 (FC); 2.3 (FC+SP); 2.8, 2,8 and 3.3 for 45, 75 and 170d, respectively
Bidner et al. (1986)	Forage (pasture) v drylot	Pasture were more yellow	Drylot thicker*	Subjective (scale as immediately above) and Objective (Hlab colorimeter, model D25)
Crouse et al. (1984)	Grass (pasture) v grain feeding (feedlot)	Grass-fed cattle more yellow**	Not given	Subjective (scale: 1 = yellow; 8 = white)
Bidner et al. (1981)	Pasture, pasture plus grain, 70d feedlot or 74d feedlot	No difference	*	Subjective (6 point scale where 3= slightly yellow; 2=tinge of yellow)
Forrest. (1981)	Pasture v feedlot 28, 56, 84 or 112d	Pasture were more yellow*	Increased from d 28 to 112*	Subjective (scale: 1 = white; 9 = intense amber) 6.5, 4.5, 3.7, 3.1 and 2.8 for pasture, 28, 56, 84 and 112 d Analytical (carotene (mg/100g fat) 0.28, 0.17, 0.13, 0.17 and 0.19 for pasture, 28, 56, 84 and 112d
Young and Kauffman (1978)	Grain v Corn silage v Haylage/corn silage	No difference	No difference	Subjective (scale: 1 = white; 5 = yellow) 3.9, 3.3 and 3.9 (s.e. = 0.36) for respective treatments (as opposite)
Dinius and Cross (1978)	Ground alfalfa hay (AH) v [concentrate (78.5% maize (corn, grain)) for 3, 6 or 9 weeks]	No difference	Increased with length of concentrate feeding*	Subjective (scale:1 = yellow; 5 = white) 2.9, 2.9, 2.6 and 3.2 (s.e. = 0.2) for AH, 3, 6 and 9 weeks, respectively.
Harrison et al. (1978)	Pasture v drylot ration [20% alfalfa haylage (common) + 75% corn (49d) or 75% corn (98d) or 36% corn: 40% corn silage (98d)]	Grass-fed (pasture) cattle more yellow*	Increased as length of feeding increased*	Subjective (scale: 1 = white; 5 = extremely yellow) 2.0 (pasture), 1.5,1.2 and 1.3 for respective diets (as opposite)
Craig et al. (1959)	Pasture inclusion v drylot ration	Drylot paler than pasture inclusion**	Not given	Analytical (Optical density/g)

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

Further evidence that changes in carcass fat colour are brought about by dilution of deposited carotenoids was provided by Knight and Death (2000). Thirty 18-month old Angus and Angus crossbred steers were grazed for 16 d on pasture (steers designated to graze turnip tops received a daily supplement of 0.8 kg pelleted barley grain per head, containing 0.5×10^6 IU vitamin A during this period) whereafter the fifteen so allocated were introduced to the turnip bulbs and fed a daily supplement of 4 kg pasture silage, 1 kg malting corms and 0.8 kg of hay per head.

Turnip-fed steers had significantly less yellow (lower '*b*' value; 9.9 v 14.3) sc fat colour ($P < 0.001$) and lower carotenoid concentration in sc fat (0.39 v 0.69 μg/g; $P < 0.001$) than their pasture-fed counterparts. As an index of carcass fatness, fat depth over the rib-eye was not significantly different between treatments,

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Table 5
Changes in sc fat subjective and instrumental colour, carotenoid concentrations and fat depth with duration of feeding

	Number of days on feedlot							s.e.
	0	28	35	42	70	105	175	
A								
Number of steers	20	–	20	–	20	20	20	
Hot carcass weight (kg)	238[a]	–	258[b]	–	282[c]	304[d]	334[c]	3.0
P8 Fat depth (mm)	12.5[a]	–	14.3[a,b]	–	14.7[a,b]	17.2[b]	17.3[b]	1.04
'b' value (sc fat)	13.7[b]	–	16[a]	–	9.8[c]	8.9[c]	8.1[c]	0.64
β-carotene (μg/g)	0.44[a]	–	0.31[b]	–	0.25[b,c]	0.17[c]	0.18[c]	0.027
Lutein (μg/g)	0.65[a]	–	0.32[b]	–	0.16[c]	0.12[c]	0.11[c]	0.019
Fat colour score	3.9[a]	–	2.4[b]		2.3[b]	1.7[b]	2.0[b]	0.25
B								
Number of steers	10	10	–	10		10		–
Carcass weight (kg)	232[a]	257[b]	–	2	278[d]	–	–	2
Fat depth (mm)	6.9[a]	7.9[a,b]	–	7.1[a]	9.6[b]	–	–	0.7
'b' value (sc fat)	16.1[a]	14.7[a]	–	14.8[a]	10.7[b]	–	–	0.5
Carotenoids (mg/g)	0.84[a]	0.66	–	0.67[b]	0.47[c]	–	–	0.06
Fat colour score	4.3[a]	4.2[a]	–	4[a]	2.7[b]	–	–	0.2

A: Data from Strachan et al. (1993); B: Data from Knight et al. (2001).
[a,b,c,d] within rows, numbers assigned different superscripts differ significantly ($P < 0.05$).

although the turnip-fed steers tended to have thicker fat (8.8 v 6.9 mm). However, the GR fat depth (over the *M. serratus dorsalis*) revealed a significant difference in fat thickness (11.2 and 15.3 mm for the pasture and turnip-fed steers, respectively ($P < 0.01$)).

The tendency for the turnip-fed steers to produce fatter carcasses is likely to have played a role in the reduced sc fat colour but the reduced carotenoid absorption (presumably resulting from reduced intake) of the turnip-fed steers relative to their pasture counterparts, as indicated by plasma carotenoid measurements, seems to have played a role in conjunction with fatness. However, Knight and Death (2000) claim that increased carcass weight and fatness played a minor role as both groups were gaining weight during the trial.

The issue of the change in bovine fat colour following feeding of a grain-based concentrate ration was also addressed by Yang et al. (1993). In that study an increase in the level of β-carotene in the sc fat was observed in the first three weeks in the feedlot, following transfer from pasture. However, no overall difference was seen in β-carotene levels between weeks 1 and 8. Furthermore, there was no change in the colour of the sc fat over the entire grain feeding period of 8 weeks. The increase in the β-carotene levels in the sc fat during the first three weeks was totally at odds with the observations of Forrest (1981) and provides a contrast to the decrease in carotenoids seen by Knight et al. (2001). The increase in the β-carotene levels in the sc fat was attributed by Yang et al. (1993) to stress following the introduction to the feedlot which may have caused increased lipid mobilisation. Increased serum cortisol concentrations corroborated this hypothesis. This would have led to relatively larger amounts of β-carotene remaining in the depleted sc fat, depending of course, on whether β-carotene was mobilised or not.

However, one noteworthy point about the steers used by Yang et al. (1993) was their age, at three years old, in comparison with the yearling steers used by Forrest (1981) and the 17 to 18-month old steers used by Knight et al. (2001). Perhaps the ability of a bovine to turnover carotenoids in its adipose tissue depends on its age, among other factors. Additionally, the steers used by Yang et al. (1993) were Brahman, a tropically-adapted *Bos indicus* genotype with potential differences in carotenoid and lipid metabolism relative to British and European continental breeds seen in more temperate climates.

Alternatively, Yang et al. (1993) stated that there may in fact have been no measurable change in total carotenoid concentrations in sc fat if carotenoids were mobilised from the fat at a rate similar to the loss of triglycerides. Strachan et al. (1993) cite Friesecke (1978) who suggested that the availability of β-carotene stored in the body for metabolism was questionable, since the half-life of the fat cell was about four weeks, although this suggestion implies that the sc fat colour of a bovine at slaughter is a reflection more of the carotenoid content of the diet in the last weeks before slaughter rather than a culmination, in terms of colour, of the entire dietary history of the animal with respect to carotenoid intakes.

6.5. Duration of concentrate feeding required to reduce carcass fat colour

Feeding of concentrates is acknowledged to reduce yellow colour in adipose tissues. General industry recommendations recognise exclusion of forage for 90 d before slaughter as a requirement to reduce yellow colour in carcass fat (Miller, 2002); this issue is of critical importance to beef producers since the length of the finishing period and the diet offered impact on profitability of beef production. However, limited information has been generated in a North-Western European situation with regard to the optimum length of time required to achieve a suitable reduction such that carcass fat colour is deemed 'acceptable' or 'acceptably pale' for lucrative Southern European beef markets. The approach usually taken in designing experiments to address this issue is a comparison involving pasture-fed cattle from which some are selected for grain-finishing for different periods where temporal changes in colour are emphasised. Such a strategy has been employed by several authors (Dunne et al., 2006; Forrest, 1981; Strachan et al., 1993) and is the usual practice employed in Australian and North American beef finishing systems (Boom & Sheath, 1997). Dunne et al. (2006) reported that 26 d feeding of concentrates were required to undo the yellowing effect of 90 d grazing for heifers but also that the choice of dietary ingredients and duration of feeding during indoor finishing would depend on the stringency of carcass colour criteria in certain markets.

Forrest (1981) conducted an experiment in which fifty yearling beef steers were reared on pasture from April to October and were then placed in a feedlot for finishing. The finishing period was 112 d and groups, each containing ten animals, were slaughtered at 28 day intervals, commencing on day one of introduction to the feedlot and subsequently on d 28, 56, 84, and 112.

The initial slaughter group of ten animals which were harvested directly off pasture were observed to have an 'amber' colour in their sc fat. After 28 d in the feedlot the amber fat colour diminished. An indication of this was that the subjective fat colour score had been reduced from 6.5 to 4.5 on a scale ranging from 1 (white) to 9 (intense amber). This coincided with a decrease in the carotene content of the fat over that same initial 28 day feeding period from 0.28 to 0.17 mg β-carotene/100 g fat.

An 'acceptable' colour of the sc fat was obtained after 56 d in the feedlot. Up to this point the fat carotene value decreased. Subsequent measurement of β-carotene in the sc fat revealed a slight increase although it was not statistically significant. Despite this, the fat colour score continued to decrease over the 112 day finishing period. Therefore, Forrest concluded that some other compound(s) and/or factors contribute to bovine fat colour. Yang et al. (1992) found that the xanthophyll lutein accounted for about 20% of the carotenoid pigmentation in bovine sc fat.

Strachan et al. (1993) conducted an experiment in which one hundred Brahman cross steers were fed a high grain diet for a finishing period of 0, 35, 70, 105 or 175 d after removal from pasture. Similar to other workers in the field (Craig et al., 1959; Harrison et al., 1978; Bidner et al., 1986) these authors found that feeding of a grain-based concentrate ration for an extended period reduced the yellow colour (both subjectively assessed and instrumentally measured) of the fat of steers relative to those on pasture, although sc fat '*b*' value increased significantly at day 35, decreasing thereafter, though not significantly (Table 5). Thus, as concluded by Dunne et al. (2006), the optimum length of finishing required to reduce yellow colour in sc fat depends on the choice of dietary ingredients and particularly the proportion of forage to concentrate but also the requirements of particular purchasers. Although graders tend to display consistency across all dates, they can be more discriminating on certain occasions when the supply of carcasses exceeds purchaser demand (Dunne, O'Mara, Monahan, & Moloney, 2004a).

7. Associations between carcass fat colour and beef quality

7.1. Nutritional effects on fatty acids and antioxidant profiles of beef

Meat quality encompasses appearance, eating (sensory) quality and also nutritional quality. Bovine diet and nutritional effects influence fat colour but also affect aspects of meat quality. There remains a perception that beef is a 'high fat' food with a high proportion of saturated fatty acids (SFA) (Moloney et al., 2001b). However, due to improved breeding, management and butchery techniques over recent decades the fat content of beef is frequently 5% or less and less than half of the fatty acids in beef are SFA (Moloney, 2002). Additionally, beef from grass-fed and forage-fed ruminants is acknowledged to have a more favourable fatty acid composition, as indicated by higher conjugated linoleic acid (CLA), n-3 PUFA and lower n-6 PUFA concentrations and a higher PUFA:SFA ratio (Nuernberg et al., 2002; Nuernberg et al., 2005; Poulson, Dhiman, Ure, Cornforth, & Olson, 2004). Cordain, Watkins, Florant, Kelher, Rogers and Li (2002) reported that tissue lipids of wild North American and African ruminants were similar to pasture-fed cattle but dissimilar to grain-fed cattle.

In addressing the question "Is beef with yellow fat potentially healthier for you than beef with white fat?" Knight and Death (1997) concluded that the health advantages of beef with yellow compared with white fat were small, despite finding that as fat '*b*' value increased, the proportion of SFA decreased ($r = -0.58$; $P < 0.001$). However, evidence suggests that the fatty acids which are enhanced by grass-feeding, such as n-3 PUFA and CLA are beneficial from a human health perspective (Williams, 2000). Hence, while yellow carcass fat can be negatively regarded in some markets, positive associations can be drawn between yellow carcass fat from grass-fed cattle and a 'healthier' beef product.

Grass has higher PUFA, including higher n-3 PUFA, primarily as linolenic acid, than grain-based ruminant feeds (Moloney et al., 2001b) in addition to being a reasonable source of vitamin E among cattle feedstuffs (McDowell et al., 1996; Wood & Enser, 1997). Mitchell, Reed, and Rogers (1991) reported that forage (pasture) fed beef had a higher proportion of n-3 PUFA than grain-fed beef. French et al. (2000b) reported that increasing the proportion of grass in the diet decreased the concentration of SFA, increased PUFA: SFA, increased the n-3 PUFA concentration (predominantly α-linolenic acid) and decreased the n-6:n-3 PUFA ratio. Ruminant-derived foods are also a rich source of CLA (Bessa, Santos-Silva, Ribeiro, & Portugal, 2000) and numerous studies have shown that using grass-or forage as the basal diet has the potential to increase concentrations of this and other beneficial fatty acids in beef (Dannenberger, Nuernberg, Scollan, Ender, & Nuernberg, 2007; French et al., 2000b; Moloney et al., 2001b; Noci, Monahan, French, & Moloney, 2005a; Noci, O'Kiely, Monahan, Stanton, & Moloney, 2005b; Nuernberg et al., 2002, 2005; Poulson et al., 2004).

Ruminants that consume grass produce meat which tends to be more resistant to deteriorative oxidative changes in colour and flavour as a result of the naturally higher vitamin E content of the grass (Wood & Enser, 1997). However, the shelf-life of beef depends not only on the absolute anti-oxidant content, but more broadly on the anti-oxidant to pro-oxidant balance (Pensel et al., 2000); this may explain inconsistencies and anomalies which are present when colour stability of grass- and grain-fed beef are compared. Descalzo et al. (2005) reported that pasture-fed steers had 1.5 times more ascorbic acid, twice the α-tocopherol concentration and 7.5 times the β-carotene concentration in *Psoas major* muscle than grain-fed counterparts. Muramoto et al. (2003) reported that steaks from β-carotene supplemented concentrate and hay-fed steers had longer colour display lives by up to 3 d, although the level of supplementation was such that daily β-carotene intake, at 7500 mg per head, was probably higher than on a grass diet. The antioxidant concentrations reported by Descalzo et al. (2005) would be unlikely to make a significant contribution to human antioxidant intake (although this would depend on the quantity and frequency of beef consumption) but may function to protect meat against oxidative deterioration and loss of red colour during retail display.

The higher levels of PUFA accumulated by grass-fed cattle, particularly in the muscle phospholipid fraction, while desirable from a human nutritional perspective, can act as pro-oxidants which may not necessarily be counteracted by higher anti-oxidant levels (Faustman, Chan, Schaefer, & Havens, 1998). Lynch et al. (2002) found that heifers that were reported to be over-wintered had higher levels of PUFA in the phospholipid fraction but produced less colour stable rib steak. Thus, while grass-feeding results in desirable modifications in muscle fatty acid composition, a priority for future research will be to optimise antioxidant protection for the beef so produced (Moloney, 2002). Although there is little doubt about an association between carcass fat colour and tissue fatty acid composition, the strength of this relationship also requires further investigation.

Among the medical and scientific community it is recognised that the imbalance between the intake of n-3 and n-6 fatty acids may be a significant contributory factor in the increasing incidence of chronic diseases in developed countries (Cordain et al., 2002; Newton, 1996; Sinclair & O'Dea, 1993) and thus, producing beef with what is construed a 'natural' diet, based largely on either fresh or conserved forage, will have potential nutritional advantages for consumers of such beef (Abbott, Basurto, Daley, Nader, & Larsen, 2004). However, a key issue in this regard is that claims that beef is grass-fed must be capable of substantiation if provenance is to be assured. Fat colour may have a key role to play in this process.

7.2. Carcass fat colour and carotenoid concentrations as an authentication tool

The potential utility of fat colour or carotenoid pigments to establish the dietary origin of meat with respect to either forage- or grain-feeding production systems requires further investigation since it may play a role in establishing the origins and dietary history of beef in the future. Traceability of animal products has become more important in recent years for a variety of reasons, including globalisation of food product distribution coupled with the potential for fraudulent claims concerning the origins, provenance and even biosecurity of some foods with the consequent potential for economic losses or damage to public health. Due to the positive relationship between fat colour and forage-feeding or between carotenoid intake and tissue carotenoid concentrations,

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measurement of either variable may represent a valuable tool for authenticating meat. Carotenoid pigments and/or their reflectance spectra in a range of tissues and products (muscle, plasma, milk, cheese) have proved effective biomarkers of grass-feeding (Prache, Priolo, & Grolier, 2003; Prache et al., 2002; Priolo et al., 2002). Taken alone or in conjunction with the contrasting concentrations of compounds such as n-3 PUFA and specific CLA and C18:1 isomers (Dannenberger et al., 2004), ascorbic acid and α-tocopherol (Descalzo et al., 2005), terpenes, sulphur compounds, phenols and other biomarkers of plant feeding (Vasta & Priolo, 2006), animal metabolites such as 2,3-octanedione (Prache, Cornu, Berdagué, & Priolo, 2005) as well as contrasting ratios of carbon stable isotopes between grass- and grain-fed ruminants (Kelly, Heaton, & Hoogewerff, 2005; Monahan et al., 2006) these provide substantial promise for traceability and authentication of fresh meat.

The distinctions which can be drawn between beef from grass-based and cereal-based finishing systems with respect to the fatty acid composition coincide broadly with differences in typical fat colour; yellow colour in bovine carcass fat is synonomous with grass-feeding which coincides with the increased n-3 PUFA and CLA already referred to. Thus, potential exists to utilise carcass fat yellow colour as a means of authentication of grass feeding but also to relate fat colour to fatty acid composition which also has broader effects on meat quality, alluded to in the previous section (e.g. colour shelf-life), as well as on human health. However, more work needs to be done in this area. Application of carotenoid spectral measurement to traceability of animal products was reviewed by Prache et al. (2005). They outlined their patented technique, whereby analysis of the reflectance spectrum of the fat in the zone of light absorption by carotenoids provides an index of traceability which can reliably and rapidly discriminate between grass-fed and grain-fed ruminants. However, most beef production systems do not rely solely on grass or grain but require varying proportions of each at different stages of production. Thus, while discriminating between cattle only receiving grass and those receiving no grass or forage, is feasible, effective practical application of these variables as an authentication tool will rely on their capability to distinguish between animals in a commercial setting, e.g. ruminants finished on concentrate diets for different periods or in varying proportions.

8. Conclusions

It is likely that the optimum finishing time on grain will be influenced by local perceptions of what constitutes an 'acceptable' colour. The length of time required to achieve an acceptable carcass fat colour, whatever that might be, is likely to depend on the age, gender and genotype of the animals, the extent of yellow colour prior to grain feeding, the rate of turnover of carotenoids in adipose tissue (although it is not known whether this occurs) and critically also the diet.

The amount of adipose tissue accumulated during grain feeding and the carotenoid and energy content of the diet are critical factors in determining carcass fat colour. Current evidence suggests that once carotenoids accumulate in adipose tissue they persist or are at least turned over very slowly. Reductions in carcass fat yellowness achieved during grain finishing of pasture-reared cattle result from a combination of (a) adipose tissue accretion which 'dilutes' carotenoids therein and (b) a low carotenoid intake on grain-based diets. However, beef from grass-fed cattle with yellow fat is not necessarily undesirable from a nutritional perspective as it has been shown to have a healthier fatty acid profile. Fat colour and carotenoid composition have potential, perhaps coupled with other characteristics and compositional features, to offer scientific verification of dietary origin, thus reducing reliance on traceability systems based solely on paper trails.

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