

Fat metabolism and regional distribution in ruminants and pigs—influences of genetics and nutrition

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Summary

In this review we first discuss the role of intramuscular fat as a factor affecting consumer preferences for unprocessed pork, beef and lamb meat. The development of intramuscular fat in beef cattle, sheep and pigs is discussed in relation to increasing carcass weight and the potential for muscle growth. It is argued that muscle development and total carcass fatness play the primary role in determining the degree to which intramuscular fat accumulates. In older animals such as mature ewes, fat turnover is also likely to exert a significant influence. The elusive target is to influence partitioning of fat between different fat depots. The influence of nutrition on the expression of intramuscular fat is discussed with the general conclusion that it is difficult to influence intramuscular fat independently of that of other depots. However, new data is presented to show that the biochemistry of intramuscular adipocytes is significantly different to that of other depots and further research will be needed to understand the significance of this.

Keywords: Intramuscular fat, muscle growth, subcutaneous fat, pig, beef, lamb

Introduction

Consumer preferences and the need to maintain profitability in the rural sector have resulted in an enormous research effort to maximise muscle deposition and minimise fat deposition in meat-producing animals such as pigs, sheep and cattle. However, leanness at all sites is not always desirable given that there are published guidelines for minimum intramuscular fat levels to secure satisfactory eating-quality outcomes for pork and red meat products. In addition, some markets will pay a premium for beef containing extra levels of intramuscular fat (marbling). In this review, we first discuss the role of intramuscular fat as a factor affecting consumer preferences for meat. The development of intramuscular fat in beef cattle, sheep and pigs is then discussed. Finally, the influence of

nutrition on the expression of intramuscular fat is discussed. The reader is referred to additional recent reviews of fat metabolism in the pig (Dunshea and D'Souza 2003) and ruminants (Pethick *et al.* 2004; Pethick *et al.* 2005c).

The role of intramuscular fat in meat palatability

Although marbling assessment is usually an integral part of beef grading schemes, the literature suggests that it only has a minor association with palatability. Dikeman (1987) concluded that marbling accounted for only 10–15% of the variance in palatability. Meat Standards Australia (MSA) research showed that although the contribution of marbling to palatability is significant, it is only one of several factors. However, Thompson (2004) concluded that as variations in tenderness are controlled by schemes such as MSA, marbling would become more important because of its specific contribution to juiciness and flavour of grilled steaks for Australian consumers.

There is also concern that very low levels of intramuscular fat will lead to meat that is perceived as dry and less tasty. Such a situation has been reported to exist for young, highly muscled, lean cattle (double-muscled cattle genotypes such as young Belgian Blue or Blonde d'Aquitaine bulls) and for many cuts of meat from modern pig genotypes (Channon *et al.* 2001). The minimum requirement for an acceptable level of consumer satisfaction for grilling of red meat (beef and lamb) is 3–4% ether-extractable fat on a fresh uncooked basis (Savell and Cross 1986) and for pork, 2–2.5% (Bejerholm and Barton-Gade 1986).

Development of intramuscular fat

Cattle and Sheep

Adipose tissue is deposited in specific depots, which are similar for all mammals. The primary depots are

within the abdominal cavity (perirenal, mesenteric and omental), intermuscular, subcutaneous and intramuscular. However, proportions differ between species and are influenced by age and total body fatness. Thus, the pig has more subcutaneous fat (70% of total body fat) and less abdominal fat than sheep or beef cattle (Wood 1984). Thompson *et al.* (1987) measured chemical fat content at all sites in mature Merino sheep and found that intramuscular fat was 7% of total body fat compared with subcutaneous fat (24%), intermuscular fat (20%), kidney fat (11%), omental fat (16%) and mesenteric fat (6%). Therefore, even in the mature sheep, the marbling depot was only of moderate to small size.

A common conclusion from animal developmental studies is that intramuscular fat is late-developing (Vernon 1981) relative to other fat depots. Indeed, the developmental order usually quoted is abdominal, then intermuscular, then subcutaneous, then finally intramuscular. However, because fat is deposited at a greater rate than lean tissues later in life, the concentration of fat in muscle will inevitably increase later in an animal's life. Therefore, the commercial trait, marbling, visible intramuscular fat or percentage intramuscular fat is late maturing. This does not mean that the rate of fat accretion in intramuscular adipocytes is also late maturing relative to that of other depots. The study of Johnson *et al.* (1972), showed that the proportional distribution of fat between carcass pools was constant over a wide range of carcass fat contents (5 kg total fat to over 150 kg total fat), indicating that the major fat depots grow in the same proportion as animals fatten. The results of Pugh *et al.* (2005) are also consistent with this observation.

The genetic relationships between fat depots or sites are known for some well-described cattle breeds such as the Angus. In this case, the genetic correlation for two different estimates of subcutaneous fat (rump vs. rib sites) is high (+0.75). There is a lower but still significant positive relationship between rib or rump fat and intramuscular fat percentage (+0.24 and +0.35, respectively; Angus Australia, 2005), which suggests that there is considerable scope for differential selection of different depots (i.e., subcutaneous vs. intramuscular).

The development of intramuscular fat relative to carcass weight in beef cattle is shown in Figure 1. The data suggests that there is a period of minimal change of intramuscular fat content at young ages, followed by a linear increase from 200–400 kg carcass weight for American Angus \times Hereford cattle (Duckett *et al.* 1993), Australian Angus cattle (Pugh *et al.* 2005) and Japanese Black \times Holstein cattle (Aoki *et al.* 2001) undergoing prolonged grain feeding. Based on this data, we propose three drivers of intramuscular fat development: (i) the potential for total carcass fat deposition, (ii) the potential for muscle growth and (iii) the extent of fat partitioning bias for intramuscular fat vs. other carcass depots. This suggests that genetic selection (via traditional

quantitative genetics or via gene marker assisted selection) for increased intramuscular fat alone could be mediated via alterations in any of the drivers described above and that a more detailed experimental approach is needed to account for this when designing genetic and/or gene marker discovery programs.

Selection for high levels of muscularity is known to reduce both total carcass fatness and intramuscular fat at a given carcass weight. Recent work with sheep has shown that lambs produced from sires with a high estimated breeding value for post weaning eye muscle depth (using the Australian Lambplan system) produce substantially leaner carcasses (Heggarty *et al.* 2005) with reduced intramuscular fat (Hopkins *et al.* 2005) compared to lambs from sires with an elevated estimated breeding value for post weaning growth rate. Mutations in the GDF8 gene of beef cattle, which effects the development of the double muscle phenotype, affect muscle development and increase muscle mass (McPherron *et al.* 1997). With respect to development of intramuscular fat, Wegner *et al.* (1998) demonstrated that the GDF8 mutant double muscled animals have fewer islands of fat cell development in their LD muscle, a lower rate of growth of these islands and smaller adipocytes in marbling islands than conventional (i.e., non GDF8 mutant) cattle. It would seem that the suppression of fat development in animals selected for muscle growth is more than just a shift in allometric development of fat and lean. Certainly, cattle breeds with a higher propensity to deposit fat have higher expression of key lipogenic enzyme either within adipose tissue (expressed per mg protein) or muscle (Bonnet *et al.* 2003), suggesting some level of metabolic down-regulation in animals selected for muscle potential.

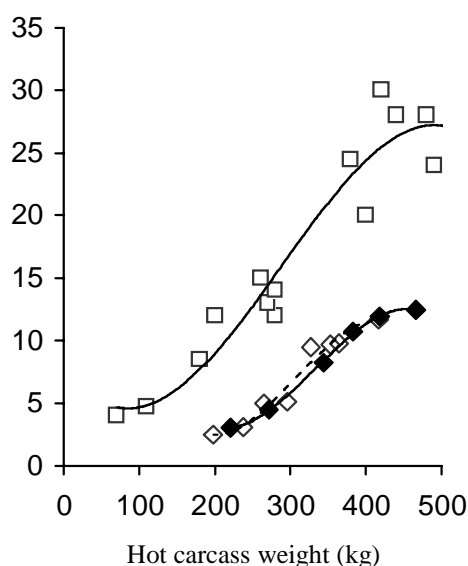


Figure 1 The relationship between carcass weight and intramuscular fat content of the *m. longissimus lumborum* of American Angus \times Hereford (\diamond , Duckett *et al.* 1993), Australian Angus (\blacklozenge , Pugh *et al.* 2005) and Japanese Black \times Holstein cross cattle (\square , Aoki *et al.* 2001).

The initial or 'starting' intramuscular fat content at ≤ 200 kg carcass weight is likely driven by the genetic predisposition for development of adipocytes at the intramuscular site relative to other depots (Figure 1). Importantly, there is a proportional developmental difference that is maintained when the American or Australian cattle are compared to the Japanese Black cross cattle: the starting (2 vs. 4%) and final (13 vs. 27%) intramuscular fat contents differ by about 2-fold. Cellular studies in rabbits (Gondret *et al.* 1998) have shown that intramuscular fat develops because of an increased number and size of clustered adipocytes with associated increases in lipogenic enzyme activity (Gondret *et al.* 1997). The cattle data suggest that the potential for cellular development of adipocytes is fixed relatively early in life and thereafter changes in either size and/or number of cells occurs in proportion to the initial cell number and/or lipogenic proteins. This indicates that a variety of 'fat' measurements taken on muscle tissue in early life have potential for predicting subsequent intramuscular fat development. Examples include intramuscular fat content (perhaps by non-invasive methods such as ultrasound) and markers of adipocytes such as fatty acid carrier proteins or functional lipogenic enzymes involved in fatty acid biosynthesis.

Another feature associated with the development of intramuscular fat is the fibre type or pattern of energy metabolism expressed by the muscle tissue. Within a genotype, the more glycolytic muscle types (e.g., *m. semitendinosus*) have lower levels of intramuscular fat (Gondret *et al.* 1998; Hocquette *et al.* 2003). A similar trend is found across different genotypes for the same muscle. Thus, in the study by Hocquette *et al.* (2003) in which two muscle types were compared across three breeds of cattle with disparate propensities to accumulate intramuscular fat, there was a strong correlation between intramuscular fat and the aerobic markers, cytochrome-*c* oxidase and isocitrate dehydrogenase, as well as adipose specific fatty acid binding protein. Admittedly, studies across genotypes that correlate the extent of anaerobic muscle metabolism to the level of intramuscular fat accumulation are confounded by the fact that highly muscled cattle are more glycolytic (Pethick *et al.* 2005d) and have less carcass fat. However, these studies as well as others in rabbits (Gondret *et al.* 2004) and sheep (Gardner *et al.* 2005) suggest that intramuscular fat content results from a balance between catabolic and anabolic pathways rather than from the regulation of a specific biochemical pathway. It has thus been speculated that a high fat turnover rate (characteristic of oxidative muscles) favours fat deposition (Hocquette *et al.* 2003).

There is little data on the development of intramuscular fat in prime lambs. However, research on the eating quality of sheep meats has shown that the level of intramuscular fat in the *m. longissimus lumborum* of crossbred Australian lamb is in the order of 4–5% on a wet matter basis (Pethick *et al.* 2005a). This value can be higher in Merino lambs (Wiese *et al.*

2005) and Merino mutton (Pethick *et al.* 2005b). Indeed, the intramuscular fat content of Australian cast-for-age ewe mutton can reach 7–12% depending on carcass fatness and animal age (Pethick *et al.* 2005b). This effect of animal age is not understood but is likely associated with different rates of fat turnover in intramuscular vs. other carcass fat depots. Thus, reproducing ewes in the Australian mediterranean environment will undergo cyclical changes in total body fatness. The hypothesis is that all depots replete during periods of high nutrition (relative to metabolic demand) but not all depots deplete fat at the same rate during weight loss periods (such as during lactation and the dry summer period).

Pigs

Selection for muscle yield has been very intense in the modern composite Australian pig, and there is a common belief that the associated reduction in intramuscular fat levels has resulted in pork that is now tougher, less moist and has reduced flavour.

The very high potential for muscle accretion in the modern Australian synthetic pig genotype seems to have had a profound influence on the development of intramuscular fat. D'Souza *et al.* (2002) reported that the intramuscular fat levels in the *m. longissimus thoracis* and *m. biceps femoris* of female pigs did not change significantly between 16 and 25 weeks of age. This would suggest that the rate of intramuscular fat deposition relative to lean muscle tissue deposition in these muscles remained constant. In other words, the linear increase in intramuscular fat deposition relative to carcass weight seen in beef cattle after about 200 kg carcass weight never occurs within the normal commercial slaughter weight window seen in pigs. The use of genotypes with Duroc bloodlines has resulted in increased intramuscular fat and improved pork quality (Blanchard *et al.* 1999). Similarly, D'Souza *et al.* (2002) reported that crossbred pigs with a high Duroc content had higher intramuscular fat levels in the loin muscle and better eating quality than crossbred pigs with low Duroc content.

Nutritional modulation of intramuscular fat

Manipulating protein and energy

Manipulation of the dietary protein:energy ratio to change intramuscular fat levels in pork has been investigated in a number of studies. The premise is that by restricting muscle development through a subtle protein deficiency, total carcass fatness will be increased sufficiently to elevate intramuscular fat. Essen-Gustavsson *et al.* (1994) showed that a deficiency of lysine increased intramuscular fat content. Cisneros *et al.* (1996) reported that a reduced dietary protein:energy ratio increased intramuscular fat levels in the *m. longissimus thoracis* of pigs. Studies by Eggert *et al.* (1998) have shown that diets supplemented with

fat during the finisher growth phase increased intramuscular fat levels of pigs and improved the eating quality of pork. D'Souza *et al.* (2003) reported that feeding a diet with either a 15% or 30% reduction in protein:energy ratio during the grower growth phase improved the intramuscular fat level of the *m. longissimus thoracis* muscle from 1.3% to 2%, which is close to the threshold (2.5%) required for optimal eating quality. Pigs fed the reduced protein:energy ratio diets had fat levels similar to those fed the control diet. However, pigs fed the 30% reduced protein:energy ratio diet had inferior feed conversion ratios compared to pigs fed the control diet.

The results of manipulating the protein:energy ratio in beef cattle diets are less conclusive. Two studies (Oddy *et al.* 2000; Pethick *et al.* 2000) concluded that diets that contain more or less protein than recommended amounts for feedlot animals do not result in significant differences in marbling or intramuscular fat. However, there was a trend for high protein diets to result in less marbling and for low protein diets to result in more marbling than control diets in both experiments. In the case of Oddy *et al.* (2000), the low protein diets in combination with added dietary fat (to decrease the protein:energy ratio) significantly decreased feed conversion ratio and cost of live weight gain relative to the control diet or the high protein diet. However, in the case of Pethick *et al.* (2000), the low protein diets did not change feed conversion ratio, perhaps because they did not include dietary fat. Certainly, the data of Pethick *et al.* (2000) suggest that a simple diet based on barley and hay (with no additional protein source) fed to Angus steers with a starting live weight of 540 kg (P8 back fat = 12 mm) resulted in performance equal to that of traditional rations containing additional protein sources at an extra cost.

Reports on the effect of supplemental fat on marbling scores in beef cattle are equivocal and are discussed by Andrae *et al.* (2001). These authors argue that marbling responses to dietary fat have been more consistent when supplemental fat was added to diets based on grains containing less fat than corn (i.e., wheat, barley). This was supported by their study in which high-oil maize (7% fat in DM) was compared to traditional maize (4.7% fat in DM) for finishing cattle (final HCW = 330 kg). Simple measures of carcass fatness (fat thickness) and intramuscular fat (visual marbling score) were similar when cattle were fed isoenergetic diets. However, when the high- and low-oil maize diets were formulated to contain identical levels of maize, the marbling score was highest for the high-oil maize ration. This was predictable because the high-oil maize diet supplied more net energy for fat synthesis.

Vitamin A

Vitamin A deficiency is associated with elevated intramuscular fat content (Harper and Pethick 2004). Indeed, recent gene marker studies with beef cattle

(Barendse 2004) have shown an association between intronic and exonic alleles within the retinoid-related orphan receptor C (γ) gene and marbling scores. It has been reported that a low intake of β -carotene or vitamin A in young Wagyu steers increases marbling (Oka *et al.* 1998). This was confirmed by Adachi *et al.* (1999), who showed that vitamin A levels in cattle blood were negatively associated with marbling scores. More recently, Kruk *et al.* (2005) observed a 35% increase in intramuscular fat of the *m. longissimus thoracis* (but not *m. semitendinosis*) in Australian Angus cattle fed a diet deficient in Vitamin A for 300 days. This was also associated with increased seam-fat thickness, suggesting that total carcass fatness had been influenced.

D'Souza *et al.* (2003) also reported that feeding pigs a grower and finisher diet deficient in vitamin A improved intramuscular fat levels of the *m. longissimus thoracis* muscle from 1.3% to 2%. It has been proposed that the effect of Vitamin A on intramuscular fat deposition is mediated by retinoic acid. This derivative of Vitamin A regulates the adipogenic differentiation of fibroblasts, inhibiting the terminal differentiation of intramuscular adipose tissue in cattle (Kuri-Harcuch 1982). It has also been proposed that retinoic acid regulates growth hormone gene expression (Bedo *et al.* 1989), which in turn decreases fat deposition and intramuscular fat in steers (Dalke *et al.* 1992). A deficiency of retinoic acid, therefore, may result in lower growth hormone concentrations and increased fat deposition, including intramuscular fat. However, D'Souza *et al.* (2003) found no change in the carcass composition of pigs (measured using dual X-ray absorptiometric analysis), suggesting that the effects of Vitamin A deficiency may be localized to intramuscular fat in the pig. However, further work to assess whole body fatness in the live animal is needed to validate this suggestion.

Fermentation pattern in ruminants

Pethick *et al.* (1997, 2004) postulated that diets that (i) promote maximal fermentation in the rumen to produce gluconeogenic precursors (propionate) and (ii) maximise starch digestion in the small intestine, might increase intramuscular fat deposition. Such diets are usually associated with high levels of processing, which increase the accessibility of the dietary starch granule to both microbial and animal amylases and consequently maximises the availability of glucose (Rowe *et al.* 1999). The premise behind this hypothesis is that (i) such diets promote increased levels of anabolic hormones (insulin), which are known to stimulate lipogenesis; (ii) in humans, diets with a high glycaemic index (i.e., diets that allow rapid glucose absorption and concomitant high insulin levels) promote obesity (Ludwig 2000); (iii) such diets will also deliver increased levels of net energy for lipogenesis; (iv) there is evidence that marbling adipocytes preferentially use glucose/lactate carbon and subcutaneous adipose

tissue mainly uses acetate as a source of acetyl units for lipogenesis (Whitehurst *et al.* 1981; Smith and Crouse 1984; Hocquette *et al.* 2005). The potential for fermentation/digestion patterns to stimulate intramuscular adipocyte development is by no means clear. Experiments are planned to test this 'glucose' hypothesis by intervening early in the life of young beef cattle (200–300 kg liveweight).

Conclusions

Intramuscular fat is clearly an important but not exclusive determinant of consumer response to pork, beef and lamb meats. A major determinant of intramuscular fat content is the potential for muscle growth. Thus, animals that display high muscle growth have reduced or no intramuscular fat during the fattening phase. In this scenario, genetic approaches for increasing intramuscular fat will need to focus on changing fat partitioning (toward intramuscular fat) if the potential for muscle growth is to be maintained. Nutritional manipulation of intramuscular fat independently from total carcass or whole body fat depots has proved difficult to achieve. However, there is now a growing body of evidence that intramuscular adipocytes are metabolically different to adipocytes at other depots (subcutaneous fat). Further research is needed to establish if this offers the possibility for specific stimulation of fat development within muscle.

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