Growth, development and nutritional manipulation of marbling in cattle

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Key findings of research

- Intramuscular fat content (% fat) or marbling score is clearly late maturing.
- However fat development within muscle is not late maturing and the expression of marbling is due to maintained fat synthesis in combination with declining muscle growth as animals get older.
- A growth curve for the development of marbling is discussed - key concepts include (i) a period up to about 200kg where intramuscular fat does not increase (ii) a period of linear development as carcase weight increases from 200-450kg and (iii) the suggestion that intramuscular fat content reaches a maximum at mature body size (around 500kg carcase weight depending of course on genotype).
- The level of intramuscular fat at the start of finishing is a key determinant of the final level of intramuscular fat after finishing. This raises the feasibility of using ultrasound estimates of intramuscular fat content at the start of finishing as a means of selecting superior marbling animals.
- The major nutritional and/or management tool for increasing the development of marbling is to maximise the availability of net energy (and glucose) for fat synthesis.
- Net energy available for fattening is the most likely reason why grain versus grass fed cattle have a higher marbling score at equal carcase weights
- In heavier 'British' type cattle (LW≥540kg, P8=12mm) it is difficult to increase the net energy for fattening by reducing protein supply (that is these cattle have a low protein requirement) and this is clearly an avenue for reducing feed costs.
- Increased processing of the ration (ie steam flaking versus dry rolling) will increase the net energy intake and glucose supply and increase marbling. The mechanism is to maximise starch digestion in the rumen (of course within animal health limits) AND small intestine and so reduce starch loss in the large intestine and faeces.
- Increased intake of dietary fat (ie high oil maize) will increase the intake of net energy and so increase carcase fatness and marbling.
- The role of fat breakdown (lipolysis) as a regulator of fat accretion is bound to be important but unknown at this time.

Intramuscular fat content (% fat or marbling) is late maturing?

A common conclusion from animal developmental studies is that intramuscular fat is late developing. Indeed the usually quoted developmental order 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 simply % fat is late maturing but we propose that this does mean the rate of fat accretion in intramuscular adipocytes is also late maturing.

To determine if there is a difference in fat deposition over time, it is informative to express the data as proportions of total carcase fat that develop within various depots, because changes in these proportions would indicate if intramuscular fat develops at a different rate from other fat depots. When fat deposition has been described in this way (Johnson *et al.*, 1972), the proportional distribution of fat between carcase pools is found to be constant over a wide range of carcase fat contents (in the range from 5 to over 150 kg total fat; Fig. 1). That is fat within muscle grows at the same rate as fat elsewhere and the reason for intramuscular fat expressing later in life is due to a declining rate of muscle growth.

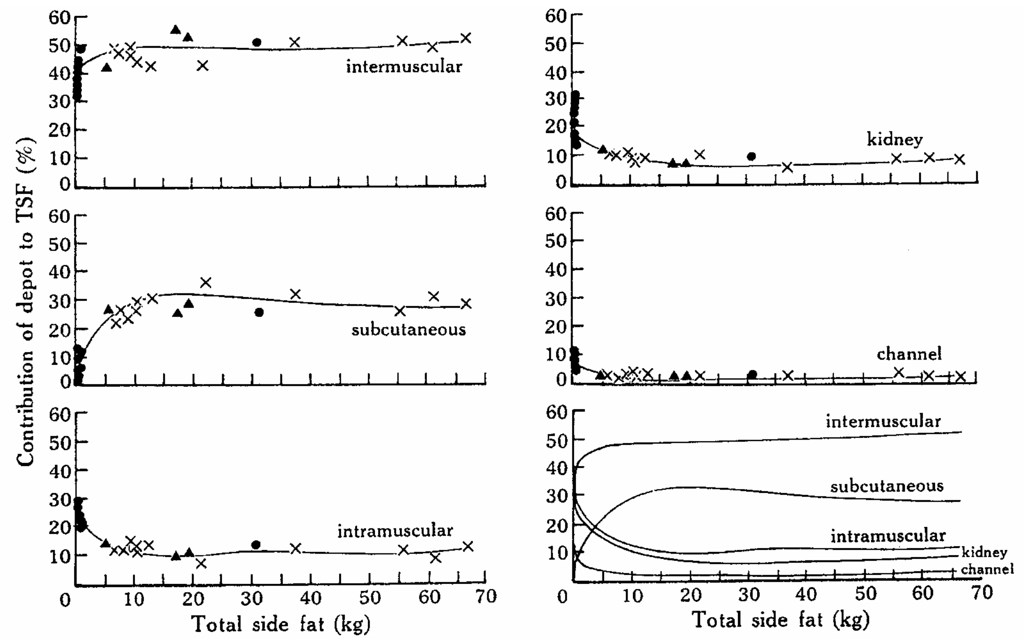

Figure 1. Contribution of individual fat depots to the total side fat. Adapted from Johnson *et al.,* 1972.

Growth curve of intramuscular fat versus carcase weight.

Theoretically we might expect the relationship between intramuscular fat and carcase weight shown in Figure 2.

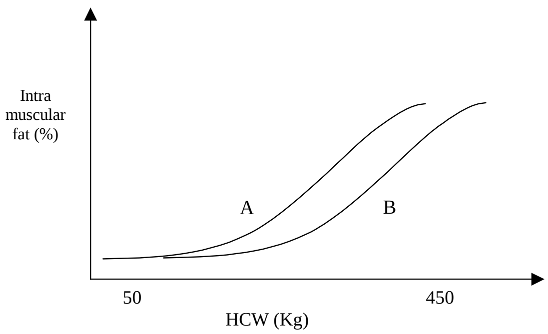

Figure 2. Hypothetical graph showing the development of intramuscular fat in cattle of different mature body weight (B>A).

The figure indicates that during the early post-natal developmental phase (around 50kg HCW) intramuscular fat content remains low and constant followed by a phase of more linear development as the carcase begins to fatten more rapidly (starting at around 200kg HCW). Finally it is assumed that as mature body size is reached (around 450 kg HCW) the increase in intramuscular fat is reduced as feed intake and growth rate decline. The actual live weight ranges at which these 3 phases of intramuscular fat development will occur would depend on the mature body size of the animal (Figure 2), and animal genotype (Figure 3).

Real data to illustrate the above curves are shown in Figure 3. The data shows that the intramuscular fat content, expressed as % fat, increases in a linear fashion between a carcase weight of about 200 - 400kg for British (Duckett *et al*. 1993) or Japanese Black x Holstein (Aoki *et al*., 2001) type cattle undergoing prolonged feedlotting. Moreover the 2 studies show that the rate of intramuscular fat (%) accretion is relatively similar such that for every 10kg of HCW intramuscular fat increases by 0.47% (Duckett et al. 1993) or 0.56% (Aoki et al. 2001) units between 200 and 400kg HCW. This is despite the data coming from different countries, production systems (although both studies used concentrate feeding) and genotypes. This confirms that an important determinant of the final level of intramuscular fat is the initial or pre-feeding level. This is an important concept because at the typical liveweight for Australian cattle entering 'marbling feedlots' (400kg) intramuscular fat content would need to be about 5% to achieve a final intramuscular fat content of 15% at 400kg HCW. This scenario should generate an AUSMEAT marble score 4.

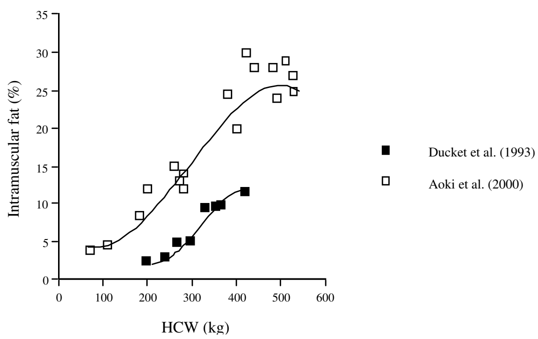

Figure 3. The relationship between carcass weight and intramuscular fat content of the *m. longissimus dorsi* of crossbred Angus x Hereford (Duckett *et al*. 1993) and Japanese Black x Holstein cross cattle (Aoki *et al*. 2000).

Intramuscular fat content at the start of finishing is important

The importance of the content of intramuscular fat at the time animals enter the feedlot is shown hypothetically in Figure 4.

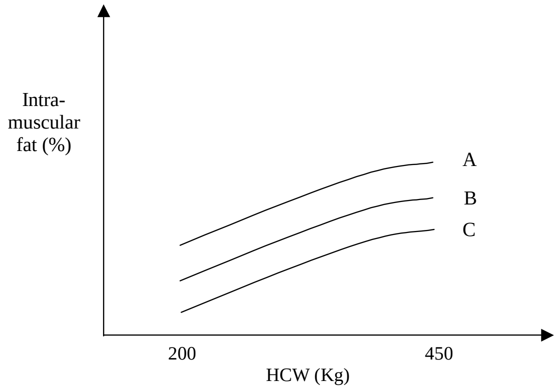

Figure 4. Theoretical pattern of intramuscular fat accretion in beef cattle - the effect of initial intramuscular fat (%) content (A>B>C) on final value in cattle of similar muscle growth potential.

Factors affecting the initial level of intramuscular fat include (i) start weight relative to mature weight (ii) genetic propensity to marble, (iii) mature body size or maturity type and (iv) pre feedlot growth rate and pattern of growth.

Implications for backgrounding and feedlotting

The implications for backgrounding and feedlotting are the sooner an animal reaches its near maximal potential for muscle and fat growth the sooner it would begin to commercially express intramuscular fat. That is fast growth throughout the animals life will result in marbling at an earlier age. A very long feeding period allows the cattle to obtain a high level of intramuscular fat since there is time for muscle maturity to be reached followed by time for the muscle to “fill up” with fat. Shorter feeding periods will have a higher risk of failure particularly if there is a relatively short period of fattening after muscle maturity is reached. The data also infer that feeding diets with an increased energy density (maximised net energy for gain) will drive greater rates of fat synthesis. In addition factors affecting the potential for muscle growth will alter the marbling response. For example animals showing compensatory growth will need longer feeding periods. Metabolic modifiers which increase the potential for muscle growth such as hormonal growth promotants, ß agonists and organic chromium would be expected to reduce the rate of deposition of intramuscular fat.

Grass versus grain

The Beef CRC studies clearly indicate that steers finished on grain have more marbling than when finished on grass. Intramuscular fat content is higher at the same carcase weight in steers finished in a feedlot rather than at pasture with a 40% reduction in intramuscular fat (%) for every 10kg HCW gained (Figure 5).

The difference in rate of increase in intramuscular fat % between pasture and grain finishing is associated with differences in deposition of fat. Dietary differences between feedlot and pasture finished animals include more net energy available for fat synthesis in the feedlot finished animals. Dietary induced differences in net energy availability include (i) greater total net intake per day in the feedlot, (ii) a decreased relative intestinal size in feedlot animals – seen as increased dressing percentage – which leads to reduced maintenance energy and thus higher net energy for gain compared with pasture fed animals and (iii) a different pattern of energy substrates available to the animal in a feedlot compared with pasture diets. Other non-nutritional factors such as less exercise in the feedlot animals resulting in a reduced basal energy expenditure and changed tissue biochemistry are also likely to be important

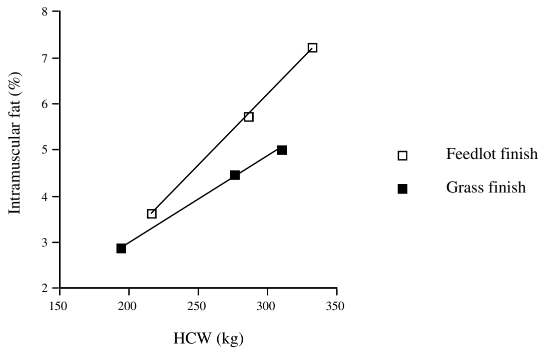

Figure 5. The relationship between HCW and intramuscular fat (%) in temperate breeds (Angus, Hereford, Shorthorn, Murray Grey) finished at 3 different market weights on either grass or in a feedlot. Analysis is based on Beef CRC data.

Feedlot finished animals received a diet of 70% dry rolled barley with average M/D = 12.1MJ ME/kgDM, and grew at between 1 and 1.8 kg /d; pasture finished animals had access to pastures of variable composition and grew at between 0.4 and 0.75 kg/d. If y = intramuscular fat and x = HCW then the relation for grass finished animals is $y = 0.019x – 0.748$ and for feedlot finished animals is $y = 0.031x – 3.045$.

Specific effects of vitamin A

The Japanese and Korean production systems produce a proportion of animals with very high levels of marbling. Whilst they utilise breeds that have high genetic potential for marbling, they may also utilise nutritional strategies that encourage marbling to develop. The feeding systems in Japan and Korea are characterised by low levels of green feed, with calves only being on green pasture for the first few months of life, followed by long grain-finishing regimens. Rice straw is also a key roughage component of the commercial diets. Carotenoids and particularly β-carotene, are metabolic precursors of vitamin A and are converted into vitamin A by the animal. Green feeds are high in β-carotene and other carotenoids, whilst roughages like rice straw are low in carotenoids.

The term ‘vitamin’, means a nutrient that is essential for survival. So vitamin A is an essential nutrient for cattle and depriving them of it will lead to a deficiency disease, and ultimately death. On the other hand, Japanese researchers (Oka *et al*., 1998) have found that the expression of marbling can be enhanced in Japanese Black (Wagyu) cattle by strategic limitation of carotenoids in the diet, inducing a reduction in the plasma levels of vitamin A metabolites. The enhancement is reversed by injection of vitamin A, suggesting the vitamin A is, or is closely associated with, the agent causing the enhancement of marbling. Oka *et al*. (1998) suggest that the animals are sensitive to strategic vitamin A limitation during the period between 18 and 23 months of age.

Vitamin A is known to act directly and strongly on cellular metabolism and body composition via some central regulatory genes. It is possible in fact, that reduced vitamin A levels could increase the number of fat cells in muscle, and hence increase the potential of muscle to marble. That is, by having more fat cells present, more are available for fat storage. Nonetheless vitamin A deficiency syndrome is a serious disease and it would be unethical from an animal welfare point of view to deliberately force animals into this state, just so that they express higher marbling. The deficiency syndrome (hypovitaminosis A) is characterised by night blindness, swollen joints and drooling. The challenge for researchers then is to find ways to manage the vitamin A nutrition of cattle so that they express fully their genetic potential to marble without allowing them to degenerate into a deficiency syndrome.

Metabolism of fat and nutritional implications

Biochemistry of fat synthesis

Finally we need to ask the question: can the rate of increase in intramuscular fat (%) be changed during the feedlotting phase? Thus far we have suggested the availability of net energy for fat synthesis as the key driver during the finishing phase. In the following sections we will explore the possibility for dietary formulation that will maximise both net energy and also possibly optimise the biochemical substrates and/or hormonal milieu that will increase lipid accretion. To discuss this question we need to understand the biochemistry of fat accretion. Fat accretion in any depot is the summation of fat synthesis and degradation. Synthesis of fat requires fat percussors called nonesterified fatty acids (NEFA) and glycerol. Glycerol is derived from glucose but the NEFA can be obtained from a variety of sources including (i) synthesis *de novo* from either glucose or acetate and (ii) they can be acquired as pre-formed fatty acids in the diet. Degradation of fat depots involves lipolysis and release of NEFA and glycerol into the circulation.

Dietary Protein/Energy ratio

Studies in rats (summarised by Webster, 1993) indicate that animals eat to maintain lean body gain, and where diets contain relatively more energy than amino acids (ie protein) they will increase intake until their “needs” for lean tissue deposition are met, and become fatter in the process. This observation has been used in pigs to increase total body fatness and intramuscular fat content (Hays *et al*, 1969; Cromwell *et al*, 1971). More recently it has been shown that deficiency of an essential amino acid (lysine) is sufficient to increase intramuscular fat content in pigs (Essen-Gustavsson *et al*, 1994). In preliminary studies using sheep Oddy et al. (1998) have shown that the amount of feed energy required to increase intramuscular fat was less in sheep eating low protein diets (Beef CRC 1998). These studies suggested that an imbalance in amino acid (or protein) supply relative to energy supply would be associated with changes in carcase fatness, and this will also impact on content of intramuscular fat.

Given this background the Beef CRC and Meat and Livestock Australia undertook two linked experiments to test the effects of dietary protein and energy density on the marbling performance of cattle fed barely based diets (Oddy et al. 2000, Pethick et al. 2000). The conclusions were that diets that contain more or less protein than recommended amounts for feedlot animals do not lead to significant differences in marbling or intramuscular fat. However, there was a trend for high protein diets to produce less and low protein diets 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 P/E ratio) significantly decreased feed conversion ratio and cost of gain relative to control and high protein diets. However in the case of Pethick et al. (2000) the low protein diets did not change feed conversion ratio perhaps because in this case they did not include dietary fat. Certainly the data suggest that a simple diet based on barley and hay (with no additional protein source in the form of grain legumes or urea) fed to Angus steers at a starting live weight of 540kg (P8 back fat = 12mm) produced equal performance to more traditionally formulated rations containing extra protein sources at an extra cost.

Substrate availability and lipogenesis de novo

Ruminants synthesise fat *de novo* in adipose tissue rather than the liver and so regulation of lipogenesis within adipose tissue is a key factor when considering fat accretion in the growing animal (Bauman and Davis, 1975). The substrates for lipogenesis *de novo* in ruminants are acetate or glucose. Given the extensive fermentation of the diet in the rumen, acetate is the major precursor for lipogenesis with a smaller contribution from glucose (Vernon,1981). The alternative pathway for lipogenesis with glucose as the primary substrate is seen in monogastric animals (ie pigs) where glucose is a major end product of digestion.

Despite the reliance on acetate as a key lipogenic substrate the availability of glucose has long been thought a limiting factor for fat accretion in ruminants (Preston and Leng, 1987; Ballard *et al.* 1972; Prior & Jacobson 1979).

Glucose availability in ruminants is largely driven by the intake of metabolisable energy with higher ME intake promoting greater rates of glucose synthesis from the volatile fatty acid propionate (Lindsay 1970; Schmidt and Keith, 1983). One possible site of further manipulation might be to use diets which promote both (i) maximal fermentation in the rumen to produce glucose percussors (propionate) and (ii) which maximise starch digestion in the small intestine. 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 so maximise the availability of both acetate and glucose to the fattening animal (Rowe et al. 1999). Evidence for this comes from Lozano et al. (2000) who showed that decreasing the flake thickness of steam flaked sorghum resulted in greater hepatic release of glucose to the general circulation. Formulating rations with this concept in mind may increase lipogenesis at the intramuscular and other sites for several reasons:

- Such diets would promote increased levels of anabolic hormones (insulin) which are known to stimulate lipogenesis.
- The logic parallels the observation in humans that diets with a high glycaemic index (ie diets that allow rapid glucose absorption and concomitant high insulin levels) promote obesity (Ludwig 2000).
- Such diets will also deliver increased levels of net energy for lipogenesis.
- There is evidence that marbling adipocytes show a preference for glucose/lactate carbon while subcutaneous adipose tissue uses mainly acetate as a source of acetyl units for lipogenesis (Smith & Crouse 1984; Whitehurst *et al.* 1981). However this is by no means conclusive given that Lee et al. (2000) could not find such differences when comparing glucose versus acetate as a substrate. Clearly more work is needed to define the metabolic profile of the intramuscular adipocytes and this is currently underway within the Beef CRC.

There is some evidence to support a link between the development of intramuscular fat and the supply of net energy and glucose (Figure 6). In the work of Pethick et al. (1997) the feeding of steam flaked maize or sorghum compared to dry rolled maize, sorghum or barley was associated with an increased content of intramuscular fat that was not simply related to changes in total body fatness alone. The steam flaked diets also induced a greater activity of a specific marker for fat synthesis from glucose (ATP citrate lyase in subcutaneous adipose tissue) indicating greater supply of both glucose and net energy (Pethick et al. 1995). The best statistical model for explaining the data is shown in Figure 6 (r^2=0.44). The model implies that dry matter intake and the activity of the glucose insulin axis (as assessed by the ATP citrate lyase activity) where factors driving both total body fatness and the expression of marbling.

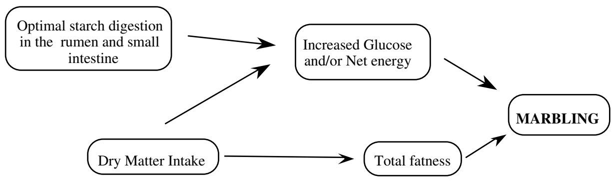

Figure 6. Statistical model to explain the influence of grain processing on glucose supply and the development of intramuscular fat (Pethick et al. 1995).

Preformed dietary fat

The other important substrate for fat accretion is preformed fat from the diet. The literature reporting the effects of supplemental fat on marbling scores are mixed and are well discussed by Andrae et al (2001). These authors argue that marbling responses to dietary fat have been more consistent when supplemental fat is added to diets based on grains that contain less fat than corn (i.e. wheat, barley) and this is supported by their study where high oil maize (7% fat in DM) was fed in comparison to traditional maize (4.7% fat in DM) to finishing cattle (final HCW = approx. 330kg). Simple measures of carcase 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 at the same inclusion level of maize the marbling score was higher for the high oil maize based ration. This is predictable since at equal inclusion in the ration along with equal dry matter intake, the high oil maize grain would supply more net energy for fat synthesis.

Lipolysis within adipose tissue

Traditionally the focus of fat accretion is on the rate of triacylglycerol synthesis from fatty acids synthesised *de novo* or obtained preformed in the diet. However for animals kept out of doors there is considerable potential for lipolytic events associated with cold or hot weather, reduced feed intake and other stressful events. Indeed fat turnover as a contributor to fat accretion is suggested by the proposed mechanism for the antilipotrophic effect of copper. Engle et al. (2000a,b) have shown that about 20ppm dietary copper reduces fat accretion in finishing cattle and a proposed mechanism is increased catecholamine activity with corresponding greater rates of lipolysis.

Lipolysis in ruminants is very sensitive to catecholamine with sensitivities in cattle some 100x greater than for pigs (Pethick and Dunshea, 1996) suggesting that managing fat turnover in ruminants might be very important. Management attributes that minimise fat turnover will in part be associated with optimising the climatic conditions for cattle. Indeed fat turnover might explain the Industry observation that marbling scores of finished cattle tend to be lower in the summer months despite maintained growth and fat depth estimates. An alternative possibility for manipulation might be to use feed additives such as niacin which reduce lipolysis at least in dairy cattle (Harmeyer and Grabe, 1981).

Summary

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- However fat development within muscle is not late maturing and the expression of marbling is due to maintained fat synthesis in combination with declining muscle growth as animals get older.
- A growth curve for the development of marbling is discussed - key concepts include (i) a period up to about 200kg where intramuscular fat does not increase (ii) a period of linear development as carcase weight increases from 200-450kg and (iii) the suggestion that intramuscular fat content reaches a maximum at mature body size (around 500kg carcase weight depending of course on genotype).
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