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Review

Muscle Energy Metabolism, Growth, and Meat Quality in Beef Cattle

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Abstract: World meat production must increase substantially to support current projections in population growth over the next 30 years. However, maximizing product quality remains a focus for many in the meat industry, as incremental increases in product quality often signal potential increases in segment profitability. Moreover, increases in meat quality also address concerns raised by an ever-growing affluent society demanding greater eating satisfaction. Production strategies and valued endpoints differ worldwide, though this makes the global marketing of meat challenging. Moreover, this variation in production schemes makes it difficult for the scientific community to understand precisely those mechanisms controlling beef quality. For example, some cattle are produced in low input, extensive, forage-based systems. In contrast, some producers raise cattle in more intensive operations where feeding programs are strategically designed to maximal growth rates and achieve significant fat deposition. Yet, others produce cattle that perform between these two extremes. Fresh meat quality, somewhat like the variation observed in production strategies, is perceived differently across the globe. Even so, meat quality is largely predicated on those characteristics visible at the retail counter, namely color and perceived texture and firmness. Once purchased, however, the eating experience is a function of flavor and tenderness. In this review, we attempt to identify a few areas where animal growth may impact postmortem energy metabolism and thereby alter meat quality. Understanding how animals grow and how this affects meat quality development is incumbent to all vested in the meat industry.

Keywords: animals; growth; muscle; meat quality; beef; tenderness; color

1. Introduction

World population is projected to reach 9 billion inhabitants by the year 2050. This dramatic growth in population will require an increase in all agricultural food commodities. Correspondingly, beef production will need to increase by nearly 60% [1] in order to feed the burgeoning global population. This increase in production will likely occur in the Southern hemisphere where production systems have the greatest capacities to increase production, either through increased capacities to add ancillary resources needed to expand the beef industry or simply by adding greater land masses [2]. However, cattle reared in the Southern hemisphere are typically managed differently and this production paradigm may lead to differences in end-product quality. Specifically, the bulk of beef produced in South American countries and Australia are fed high forage-based diets. Even when more intense feeding programs are attempted, these systems are less aggressive compared to cattle fed under more

intensive feeding paradigms. Therefore, cattle growth and meat quality should be explored to better understand the potential opportunities and challenges in expanding beef production worldwide.

While there have been a myriad of exhaustive reviews on beef cattle production and meat quality [3,4], the focus of this short review is to identify a couple of areas where additional information may be necessary in order for the community of meat scientists to offer reliable assistance to our colleagues attempting to maximize beef production systems across the globe. It is important to understand, however, that various production systems throughout the world have evolved largely in response to a myriad of factors including, but not limited to, cultural, societal, and political pressures. To suggest, imply, or otherwise advocate that one system should be adopted as the norm for meat production worldwide would be imprudent and cavalier.

2. Muscle Growth

Muscle formation begins early in fetal development. Russell and Oteruelo [5] determined that the majority of skeletal muscle fibers begin to develop within the first two months of embryonic development in cattle and this continues well into the seventh month of gestation [6]. Yet, when a calf is born, it is no longer able to create new muscle fibers [7]. Rather, the existing muscle fibers continue to grow through hypertrophic mechanisms [8], largely yet to be understood [9]. Nonetheless, muscle is a heterogeneous collection of muscle fibers that vary in their ability to function and metabolize energy [10]. At the same time, these fibers experience differing abilities to grow in volume [11]. Briefly, muscle fibers are broadly characterized into fast and slow-contracting fibers, which are largely based on the type of myofibrillar and regulatory proteins in each muscle fiber [12]. Fibers are also categorized by the relative differences in the predominate type of metabolism existing within the fiber as compared against other muscle fibers across a given muscle. As mentioned, speed of contraction is not simply a function of the myosin molecular structure [13], but often for the sake of simplicity and gross estimation, fibers are largely classified by the predominate myosin heavy chain [14]. To that end, slow-contracting fibers consist mainly of type I myosin heavy chains (MyHCs), while fast-contracting fibers consist of either type IIa, type IIx, and type IIb MyHCs, and correspondingly, vary in their abundance of glycolytic-based enzymes and substrates (IIa < IIx(d) < IIb) [14]. It is important to understand that while this approach provides great insight into the nature of various factors that affect meat animal production, the mechanisms responsible for these differences are occasionally clouded by the overall lack of crispness in defining muscle fiber type or even muscle type. Further, the muscle studied is somewhat limited in its use for understanding the changes in overall production efficiency of an animal. Regardless, while animals are generally born with a higher proportion of slower-contracting, type I fibers, the composition of fibers within a muscle generally begins to shift collectively from a more oxidative to a glycolytic nature of metabolism during the process of hypertrophy [14,15]. This shift in the cues responsible for this change in muscle heterogeneity may be an interesting area of greater exploration in the future.

While this review is mainly focused on beef cattle, the best success story for improving growth efficiency is the modern day broiler (chicken). Today, most integrators produce meat chickens in a third of the time required to achieve the same weight in 1957, with only a third the amount of feed. While remarkable, what are the biological mechanisms responsible for achieving such progress? The pectoralis major muscle tends to consist predominately of type IIb muscle fibers that are large in diameter and more glycolytic in nature. At the same time, cattle tend to have more oxidative muscle fibers [16]. In fact, cattle muscle lacks any discernable type IIb fibers, yet the gene resides in the cattle genome [15]. Therefore, are fast-contracting, glycolytic fibers required for improvements in growth efficiency? If so, what are the cellular mechanisms for these changes?

3. Nutrition

We have known for some time that maternal restriction of nutrients during the early stages of pregnancy compromises embryonic and fetal growth. Restriction of nutrient intake through any

number of different forms during the early stages of pregnancy reduces the number of muscle fibers, thereby reducing muscle mass and postnatal performance [17,18]. Similarly, a reduced supply of nutrients during critical stages of development may impact the formation of adipocytes, which largely form the basis for intramuscular fat deposition and meat palatability [17]. Therefore, feed restriction of pregnant cows can have a detrimental impact on the postnatal growth rate and meat quality.

During postnatal growth, providing appropriate levels of nutrients throughout all stages of an animal's life is critical to achieve an optimal growth rate and produce the highest quality product possible. However, in some feeding paradigms, maximal growth rate is not achieved and may not even be the goal. For example, in less intensive, low input pasture-based production systems, feed restriction often occurs, and nutrient intakes are well below the requirements needed for optimal growth [6]. In fact, nutrient intakes are often well below requirements, and this affects animal performance, lean tissue deposition, and composition, as well as meat quality traits to different levels depending on the stage of life that it occurs in the animal [19]. In pasture-based systems, energy intake above that needed for maintenance is used for tissue deposition (muscle and fat) but is generally limited, leading to slower growth rates and fat deposition when compared with feedlot finished animals. This slower growth rate is generally associated with lowered meat quality depending on the benchmarks used to assess and define quality. However, this nutrient restriction can also affect performance in different ways, depending on the severity and the stage in which it occurs.

Differences in the nutritional plane also influence muscle fiber type composition. Specifically, pasture-fed animals were shown to have a higher frequency of slow-twitch oxidative fibers and a lower frequency of fast-twitch glycolytic fibers compared to feedlot-finished animals [20]. Furthermore, Gagaoua et al. [21] showed a switch to a more oxidative fiber type (MyHC-IIa) at the expense of fast-twitch glycolytic fibers (MyHC-IIx) in grass-fed animals compared to those fed hay or haylage. In contrast, an increase in metabolizable energy intake led to an increase in live weight gain and induced a higher frequency of fast-twitch glycolytic fibers [22]. In addition, studies have confirmed a positive correlation between dietary energy level and the proportion of glycolytic fibers in cattle [23–25]. Moreover, increasing nutrient intake after a period of dietary restriction shifts muscle metabolism toward a more glycolytic type [26], arguing that a positive relationship exists between growth and fast-contracting fibers. However, when cattle go through a period of energy restriction, a decrease in muscle fiber size is observed on all fiber types, especially on fast-twitch glycolytic fibers [11]. Therefore, understanding the effects of feeding paradigms on muscle fiber type and composition and growth is warranted. Of course, these changes in muscle fiber type composition have some impact on meat quality traits, such as color and tenderness. Oxidative muscles are known to have a decreased rate and extent of postmortem pH decline and lightness [27,28] and inherently have an increase in redness due to a higher myoglobin concentration [29], thus resulting in darker meat when compared to glycolytic muscles.

The relationship between muscle fiber type and tenderness is still quite controversial. An increase in meat tenderness was observed as the frequency of type I fibers increased along with a decrease in the percentage of type IIx in cattle [30]. In contrast, Kovanen et al. [31] reported that slow-contracting muscles contain more collagen, which plays an important role in the binding of muscle fibers and decreases meat tenderness. Renand et al. [32] showed that bovine muscles with larger fibers, especially type IIx fibers, exhibited tougher meat than muscles with smaller muscle fibers, such as those of oxidative fibers. However, a positive correlation between tenderness and fast-glycolytic fiber frequency has been noted in cattle [33], which may be due to a higher calpain/calpastatin ratio in fast-twitch glycolytic muscles, partly explaining the faster rate of aging in glycolytic muscles [34]. Either way, considerable information is lacking in the area of meat tenderness (covered more below) and muscle growth and fiber type composition.

4. Postmortem Metabolism

Following stun and exsanguination, muscle labors to maintain ATP homeostasis. However, ATP turnover is quite high postmortem and, in an effort, to regulate ATP loss, the phosphagen system immediately activates postmortem [35]. Phosphocreatine (PCr) re-phosphorylates ADP to ATP using the enzyme creatine kinase (ADP + phosphocreatine → ATP + creatine). In addition to maintaining ATP levels, creatine kinase consumes hydrogen ions (H+), thereby partially buffering pH decline postmortem. However, the phosphagen system is incapable of maintaining ATP homeostasis for an extended time. Once 70% of PCr is consumed, ATP decreases rapidly in the muscle tissue [36]. This decrease in ATP, or more specifically, increase in ADP, triggers glycolysis in an effort to create more ATP and allows the muscle to stay in a relaxed state [37].

During this entire process, ATP is continually hydrolyzed, releasing H+ ions and inorganic phosphate (Pi). Similarly, H+ ions accumulate in muscles during a bout of exercise, but these ions are partially consumed by the formation of lactate and its removal by the circulation. Ultimately, these substrates (carbons) are made available to the muscle in the form of glucose through the Cori cycle [38]. In postmortem muscle, however, conversion to lactate remains the sole source of buffering hydrogen ion accumulation in muscle, but with time, these ions ultimately lower muscle pH from 7.0 to 5.7–5.5 within 24 h. Acidification of muscle is absolutely mandatory for the development of the typical color and textural properties of fresh beef. When abbreviated, fresh beef appears dark and has a firm and dry (DFD) texture. Yet, if metabolism is accelerated postmortem, carcass temperatures are elevated and the pH decline is greater [39,40]. This combination of low pH and high temperature results in excessive protein denaturation and a product with impaired water binding ability and color, leading to an inferior product, though its occurrence is rare in the transformation of cattle into beef [41].

Conversion of muscle to meat has traditionally been thought to be an anerobic process due to the inability to deliver oxygen to the mitochondria, yet mitochondria function postmortem [42,43]. Scheffler et al. [44] first proposed the possibility of mitochondria influencing postmortem metabolism using an in vitro system [45]. Specifically, these investigators found that addition of mitochondria to glycolyzing reactions increased the rate of ATP loss and attributed this to the F_1F_0-ATP synthase functioning in reverse and acting as an ATPase. Matarneh et al. [46] attributed the role of mitochondria, in part, as the mechanism for pH breaching the normal set points of the ultimate pH of muscle. This flux in pH is because F_1F_0-ATP synthase, or complex V of the mitochondria, disassociates postmortem [47] and allows the F_1 subunit to hydrolyze ATP at levels below those environments normally permissible for most myofibrillar ATPases [48]. While the exact role the mitochondria plays postmortem remains obscure, these data argue that the mitochondria may affect ATP homeostasis postmortem and may affect pH decline and, ultimately, meat quality attributes, perhaps even in those cattle fed in differing finishing systems across the globe.

Grazing animals possess lower concentrations of muscle glycogen at the time of slaughter, leading to an inadequate carcass pH drop after slaughter, impairing meat color, tenderness, and shelf life. Immonen et al. [49] found a lower muscle glycogen content in cattle fed only hay compared to cattle fed a high grain diet. Administration of a short-term, high-energy diet is an effective strategy to reduce glycogen loss prior to slaughter and improve the final pH [50]. Knee et al. [51] also proposed that the supplementation of cattle fed low-energy forage with a grain-based feed for three weeks prior to slaughter reduces the incidence of DFD due to an increase in muscle glycogen. In addition, McGilchrist et al. [52] reported that a higher rate of growth, achievable by the administration of a high-energy diet, may reduce the incidence of DFD due to an increased glycogen content.

5. Meat Quality

Consumers use lean color as an indicator of freshness and quality [53]. Though meat color and quality are not well-correlated [54], consumers consider beef color to be one of the most important attributes when purchasing it [55]. Yet, 15% of all retail beef cuts fail to meet the expectations associated with the bright cherry red lean designation [55,56]. This lack of acceptable lean color costs the industry

nearly $1 billion dollars annually in the United States alone [55]. While lean color is key in making purchasing decisions, beef tenderness has shown to be the most important quality attribute when consuming beef [57], and similar to undesirable beef color, 25% of commercial beef does not meet consumer expectations in regard to tenderness [58].

5.1. Color

Variations in fresh beef quality are impacted by a number of inherent physiological aspects of the animal including, age, sex, breed, growth rate, and nutrition [59]. However, meat color is heavily predicated by the abundance of the pigment protein myoglobin [60]. Myoglobin is a water-soluble protein responsible for transporting and storing oxygen from the blood to the muscle [61]. Due to muscle variation in metabolism and energy demand, the myoglobin concentration differs not only between species, but also between muscles [62]. Endurance muscles and muscles that are more fatigue resistant, such as muscles located near the bone, need oxygen, as they tend to be rich in mitochondria and utilize oxidative metabolism as a source for energy production. Due to the muscles' need for oxygen, myoglobin is in high abundance and causes the muscle to have a deeper red color [63]. Glycolytic muscles are typically muscles used for quick bursts of energy, and because oxygen is not required for their function, myoglobin abundance is lessened [64], giving the muscles a lighter or paler appearance.

In general, beef and other ruminants produce meat that is darker than their differing counterparts—monogastric animals. This difference has been largely attributed to differences in myoglobin content, or its lack thereof [65]. Curiously, beef from cattle predominately fed grass diets produce even darker lean meat than their concentrate-fed counterparts [20,66–68]. While many argue that a lack of glycogen metabolism leads to a modified dark cutting beef phenomenon, grass-fed cattle have more oxidative muscle than those cattle finished on a concentrate diet [23]. Moreover, glycolytic flux (glycolysis) appears to stop earlier in redder, more oxidative muscles and thereby results in a higher than normal ultimate pH, independent of glycogen availability [64]. As muscle grows and experiences hypertrophy, it becomes more glycolytic or less oxidative, although fiber type composition is highly variable between individuals of the same breed reared under similar nutritional and environmental conditions [12]. Indeed, cattle that are fed high forage diets grow slower than cattle fed high concentrate diets [69,70], suggesting that lean meat from grass-fed cattle differs from that of high-concentrate fed cattle, and raises the argument that the latter possess muscle that is more glycolytic and therefore more resistant to generating dark color lean meat. Alternatively, this also argues that darker beef originates from cattle lacking sufficient energy intake, or kind, to change their muscle to a more glycolytic type.

5.2. Tenderness

Meat tenderness is impacted by the pH [71–75]. In fact, when coupled with temperature, the rate and extent of pH has shown to create an ideal "window" for meat tenderization in beef. This ideal relationship is optimized when a carcass maintains a pH greater than 6.0 while the carcass temperature remains elevated above 35 °C. Further, as a carcass begins to chill, the pH must drop below 6.0 prior to temperatures falling below 12 °C [76]. Although it is well established that meat tenderization is a result of Ca^{2+} activated calpain proteases and their ability to degrade myofibrillar proteins along the Z disks, this ideal "window" is likely related to μ-calpain activation under conditions of high pH. Maddock et al. [77] determined that μ-calpain activation is highest at pH 6.5. While pH 6.5 cannot be maintained during normal pH decline, Hwang and Thompson [78] determined that calpain activity is optimized when an intermediate pH decline is achieved with the pH reaching 6.0 at 1.5 h postmortem. Furthermore, Lomiwes [74], compared proteolysis between high and low ultimate pH (pH(u)) myofibrillar proteins. *Longissimus dorsi* muscle, isolated from bulls 24 h postmortem and aged, showed differences in proteolysis. The results illustrated that high pH(u) beef underwent rapid tenderization in the early postmortem period, whereas low pH(u) beef underwent later degradation

of myofibrillar proteins. This difference in the rate of proteolysis is likely attributed to the increased activation of μ-calpain at a high pH, while μ-calpain influences the initial proteolysis of titin and nebulin in the early postmortem period. Much of the tenderization in low pH(u) beef comes from residual μ-calpain activities during the aging process. However, a rapid decline in pH inactivates μ-calpain as well as other key enzymes due to extreme denaturation, ultimately inhibiting postmortem proteolysis [79].

The calpain system also comprises an additional protein, calpastatin. Calpastatin is a specific inhibitor of μ-calpain and can blunt proteolysis. The calpain to calpastatin ratio alters the rate and limit of meat tenderization [80], making it difficult to produce consistent beef as calpastatin levels vary across breeds [81,82], muscle types [83], and the presence of growth promotants such as beta-agonists [80,84].

While pH and μ-calpain influence beef tenderization, it is difficult to control because so many factors can alter the rate and extent of proteolysis, specifically feeding regimes. Currently, there is much debate in the literature regarding concentrate and forage-finished cattle and the ensuing tenderness of meat. Bruce et al. [85] compared differing extensive feeding strategies (124 d or 175 d) of concentrate and forage diets and found that steers fed high energy diets produced carcasses with increased tenderness, regardless of the days given feed compared with forage-fed beef. These data are in agreement with many studies [86,87], yet others have shown no difference in meat quality between grain and forage-finished beef, including tenderness [88,89]. At the same time, however, others have reported lower shear force values in meat from grass-fed animals than from those fed with concentrate [90,91]. It has been hypothesized that the greater vitamin E content in meat of pasture-fed cattle increases the collagen turnover due to greater expression of matrix metalloproteinases, which improve meat tenderness [92]. Validation of this hypothesis remains forthcoming.

It is important to note that the effects of different feeding systems may not influence the tenderness of all muscles in a similar way [93]. While diet may influence beef tenderness at times, it is typically confounded by other factors that have also shown to influence tenderness, such as age, growth rate, carcass weight, and external fat cover. This suggests that diet may not independently influence tenderness. In addition, the combination of degree of physical activity and feeding strategy affect muscles of different metabolic properties to a different extent [93]. Regardless, further investigation into the exact role of how nutrition, age, growth, and exercise influence beef quality is well warranted.

6. Conclusions

A variety of beef production systems have emerged across the globe for a number of reasons. However, animal performance targets differ based on the production paradigms implemented. Whether those differences in beef quality characteristics observed, regardless of the metrics used, are simply a result of divergent management schemes or are truly indicative of underlying mechanisms resulting from differences in growth rate warrants further exploration. To anticipate and respond to projected increases in the global demand of beef, we must understand, in detail, those mechanisms responsible for optimizing lean beef production and maximizing its quality, regardless of where it is produced.

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