Heat Adaptability and Tenderness

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Beef from *Bos indicus* cattle is associated with more variation in toughness compared to *Bos taurus* breeds, indicating there is antagonism between thermotolerance and beef palatability. However, the physiological connections between heat tolerance and tenderness are poorly understood. By virtue of its contribution to body weight, muscle may play an important role in defining the thermoregulatory capacity of *Bos indicus* cattle. Ultimately, defining relationships between muscle metabolism and heat tolerance are necessary in order to optimize growth and tenderness, without sacrificing the heat tolerance of *Bos indicus* breeds.

What Factors Affect Heat Tolerance?

Compared to *Bos taurus* cattle, *Bos indicus* cattle have an improved ability to regulate body temperature in response to heat stress. Heat tolerance is a function of the capacity for heat loss, and the heat production from metabolic processes. Heat transfer between the animal and the environment is dependent on surface area of the animal per unit weight, the temperature gradient between the animal and the air, and the properties of the hair coat. For example, Brahman possess smooth, slick, light-colored hair coats that reflect solar radiation, thereby preventing heat absorption by the animal. Additionally, heat loss can occur through evaporative mechanisms, such as sweating or panting.

Conversely, heat tolerance is also influenced by metabolic rate or heat production of the animal. In turn, metabolic rates determine the nutrient or energy requirements, and growth rates of livestock. A portion of the nutrients an animal consumes is lost through feces, urine, and methane. The remaining metabolizable energy is allocated for basal energy expenditure, which is the energy needed for maintenance of cellular functions within the animal; and for the energy required to do work. Specifically, once the energy requirements for digestion of food and physical activity are met, the 'leftover' energy can be dedicated to production (e.g., growth or milk). Accordingly, higher producing animals have greater nutrient requirements and metabolic rates, and thus possess a reduced capacity to adapt to environmental heat stress. While Brahman clearly have properties to enhance heat loss, there is also evidence to support that decreased heat production contributes to their heat tolerance.

Are Metabolic Rate, Growth, and Tenderness Related?

Reductions in basal metabolism and growth rate appear to contribute to decreased metabolic rate of *Bos indicus* breeds. Metabolic rate is determined by heat production of different organs and tissues of the animal. Some organs, such as the brain or liver, represent a low percentage of body weight, but exhibit high metabolic activity. In contrast, muscle is not particularly active on a per unit basis, but contributes significantly to metabolic rate since it represents roughly 40% of body weight.

On a cellular level, nutrients from the diet are metabolized to accomplish vital functions, including protein synthesis, muscular contraction, and the maintenance of ion gradients across membranes. However, the energy demand does not come from these processes; rather the additional energy required for cellular maintenance is due to processes that oppose these functions (reviewed by Rolfe & Brown, 1997). These opposing or uncoupling processes include protein degradation, muscle relaxation, and ion leaks. Consequently, decreasing any of these uncoupling processes would be expected to decrease the animal's metabolic rate and energy requirements. Accordingly, the decrease in metabolic rate would be dictated by which organs are impacted, as well as the extent to which uncoupling processes are reduced.

Interestingly, there is evidence that *Bos indicus* cattle have lower protein degradation in muscle, which would help explain not only reduced growth rates and metabolic rates, but also tougher beef. Muscle growth is an energetically demanding process; in order to increase muscle mass, proteins must be synthesized as well as degraded, which is also known as protein turnover. The net balance of synthesis and degradation dictates the gain in muscle mass. In living muscle, several systems contribute to protein degradation; of these, the major player in postmortem muscle is the calpain-calpastatin system. Calpain cuts proteins into fragments, which disrupts the structure of muscle cells and contributes to the tenderization of beef. Calpastatin, on the other hand, is the only known inhibitor of calpain (reviewed by Goll et al., 2003). *Bos indicus* cattle are well-documented to possess elevated calpastatin activity in postmortem muscle, consequently decreasing degradation and limiting tenderization (Wheeler et al., 1990; Whipple et al., 1990; Pringle et al., 1997). Thus the greater calpastatin observed in muscle of Brahman and *Bos indicus* breeds may be a mechanism for limiting protein turnover in the animal, in order to restrict metabolic heat production; in postmortem muscle this manifests as tougher beef. Certainly, it is possible that other organs of *Bos indicus* cattle also contain greater calpastatin or that other mechanisms to prevent protein degradation are upregulated, but these data have not been reported.

Besides protein degradation, changing cell size may be another mechanism for reducing metabolic cost. Increasing cell size reduces the surface area to volume ratio, which decreases the cost of maintaining the membrane potential (Jimenez et al., 2013). This affects the activity and distribution of ion pumps at the membrane, thereby reducing the energy required for cell maintenance. Increasing percentage of Brahman genetics was associated with larger type IIx muscle fibers (Wright et al., 2018). Greater toughness may be related to larger fiber size (Chriki et al., 2012). Yet, as protein degradation increases during aging, the effect of fiber size on tenderness is less pronounced (Crouse et al., 1990).

Basal metabolic rate is also affected by proton leak in the mitochondria, the energy producing organelles of cells. Proton leak in mitochondria increases metabolic rate and heat production, but uncouples fuel oxidation from energy production. Reducing proton leak in mitochondria may be another mechanism to restrain heat production in *Bos indicus* cattle. The connection between mitochondria and meat quality development is less clear, but this is an active area of investigation. Disruption of mitochondria early postmortem is associated with initiation of proteolysis and greater tenderization. Some have suggested that disruption of mitochondria stimulates cell death pathways, which, in turn, activates enzymes capable of degrading calpastatin (Kemp et al., 2010). This is an attractive concept because enhancing calpastatin breakdown would hasten tenderization. However, this is a controversial topic as others have reported that there is no evidence that this process occurs in muscle postmortem (Mohrhauser et al., 2011; Underwood et al., 2008).

Furthermore, *Bos indicus* breeds may have acquired other mechanisms to protect against cellular stress. In response to elevated temperatures, cells produce heat shock proteins to help stabilize and protect cellular structures. In postmortem muscle, structural protection by heat shock proteins may hinder the breakdown of muscle, thereby limiting tenderization. Along these lines, loin muscle of Brahman cattle exhibit greater resistance to metabolic changes postmortem, demonstrated by slower pH and energy decline (Ramos et al., submitted). Additional work is ongoing to determine underlying mechanisms.

Conclusions

Bos indicus cattle impart heat tolerance, but have garnered a reputation for slow growth and variation in palatability. Certainly, there is tremendous economic incentive to increase growth performance and improve product consistency. Because muscle represents a significant portion of body weight, shifts in metabolism may contribute to heat production and thus affect the thermoregulatory capacity of *Bos indicus* cattle. On a cellular level, there are several possible connections between heat tolerance and tenderness, including but not limited to, calpastatin, mitochondrial function, and heat shock proteins. Defining the relationships between muscle characteristics and heat tolerance are critical to developing strategies that optimize growth and tenderness without sacrificing heat tolerance of *Bos indicus* breeds.

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