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BOARD INVITED REVIEWS

Cattle adapted to tropical and subtropical environments: social, nutritional, and carcass quality considerations

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Abstract

Beef production needs to increase from 60 million to 130 million tons by 2050 to feed a growing world population, and 70% of this production increase is expected from beef industries located in subtropical and tropical regions of the world. *Bos indicus*-influenced cattle predominate in these regions but are often managed using practices developed for *Bos taurus* breeds reared in temperate climates. Hence, a fundamental step to meet the increasing global demand for beef is to develop specific management for *B. indicus*-influenced cattle in tropical or subtropical environments. *Bos taurus* and *B. indicus* are different subspecies, and diverge in social and biological functions due to selection pressure caused by complex evolutionary and domestication processes. *Bos indicus* cattle display different social responses compared with *B. taurus* counterparts, which must be taken into account by management planning as these traits directly impact cattle performance and welfare. In tropical and subtropical regions, warm-season perennial C4 grasses are the dominant forages, and their availability has a significant influence on the productivity of beef cattle systems. The resilience of C4 grasses under adverse conditions is one of their most important characteristics, even though these forages have reduced nutritive value compared with forages from temperate climates. Accordingly, nutritional planning in tropical and subtropical conditions must include management to optimize the quantity and quality of C4 forages. Nutritional requirements of cattle raised within these conditions also require special attention, including inherent metabolic compromises to cope with environmental constraints and altered energy requirements due to body composition and heat tolerance. Nutritional interventions to enhance beef production need to be specifically tailored and validated in *B. indicus*-influenced cattle. As an example, supplementation programs during gestation or early life to elicit fetal programming or metabolic imprinting effects, respectively, yield discrepant outcomes between subspecies. *Bos indicus*-influenced cattle produce carcasses with less marbling than *B. taurus* cattle, despite recent genetic and management advances. This outcome is mostly related to reduced intramuscular adipocyte volume in *B. indicus* breeds, suggesting a lesser need for energy stored intramuscularly as a mechanism to improve thermotolerance in tropical and subtropical climates.

Key words: behavior, *Bos indicus*, carcass, forage, nutrition, tropical and subtropical environments

Abbreviations

AFT	adjusted fat thickness
BRD	bovine respiratory disease
bST	bovine somatotropin
CSSO	soybean oil with Ca salts
EW	early weaning
FA	fatty acids
HA	herbage allowance
HP	heat production
i.m.	intramuscular
ITM	injectable trace minerals
MEI	metabolizable energy intake
NADP-MDH	NADP-malate dehydrogenase
PDF	probability density functions
peNDF	physically effective NDF
s.c.	subcutaneous
SBW	shrunk BW
SCD	stearoyl-CoA desaturase
TMR	total mixed ration

Introduction

According to the United Nations, food production must double by 2050 to meet the demand of the world's growing population (FAO, 2009). Nonetheless, at least 1 billion people still experience inadequate intake of protein, and 165 million of these individuals are children. Resources for food and agriculture production will also become more limited as the planet becomes more populated and urban areas expand. Therefore, agricultural efficiency must increase dramatically during the next decades to meet the global food demand while maintaining ecological stewardship and proper use of limited natural resources.

Global meat consumption is also expected to increase by 30%, which will require a 72% increase in current meat production by 2050 (FAO, 2009). Beef represents 25% of the total meat produced worldwide, and its consumption is projected to increase from 60 million to 130 million tons by 2050. At least 70% of the increase in beef production required to meet the growing demand is expected to come from subtropical and tropical regions of the planet (FAO, 2009), including southern United States, Mexico, Central/South America, Africa, Asia, and Oceania. These regions contain more than 80% of the world's cattle population (Figure 1), predominately *B. indicus*-influenced breeds with diets based on forages and agricultural byproducts (Robinson et al., 2014; FAOSTAT, 2019). In the United States, approximately 45% of beef cows are located in the southern and southeastern states, where *B. indicus*-influenced cattle are located and tropical/subtropical climates predominate (NASS, 2017).

Bos indicus-influenced herds reared in subtropical and tropical regions are often managed using practices developed and validated for *B. taurus* breeds in temperate environments. *Bos indicus* and *B. taurus* are two individual subspecies and differ in several body functions related to beef production, including reproductive physiology, nutritional needs, social behavior, digestive system, and body composition (Turner, 1980; Table 1). Hence, a fundamental step to meet the increasing global demand for high-quality protein is to understand these differences and develop management practices tailored to cattle reared in subtropical and tropical regions. This manuscript provides a review of historical and contemporary research focusing on social, nutritional, and carcass quality considerations related to the production of *B. indicus*-influenced cattle within the planet's subtropics. A similar review focusing on genetic aspects and reproductive parameters is presented by the companion manuscript (Cooke et al., 2020).

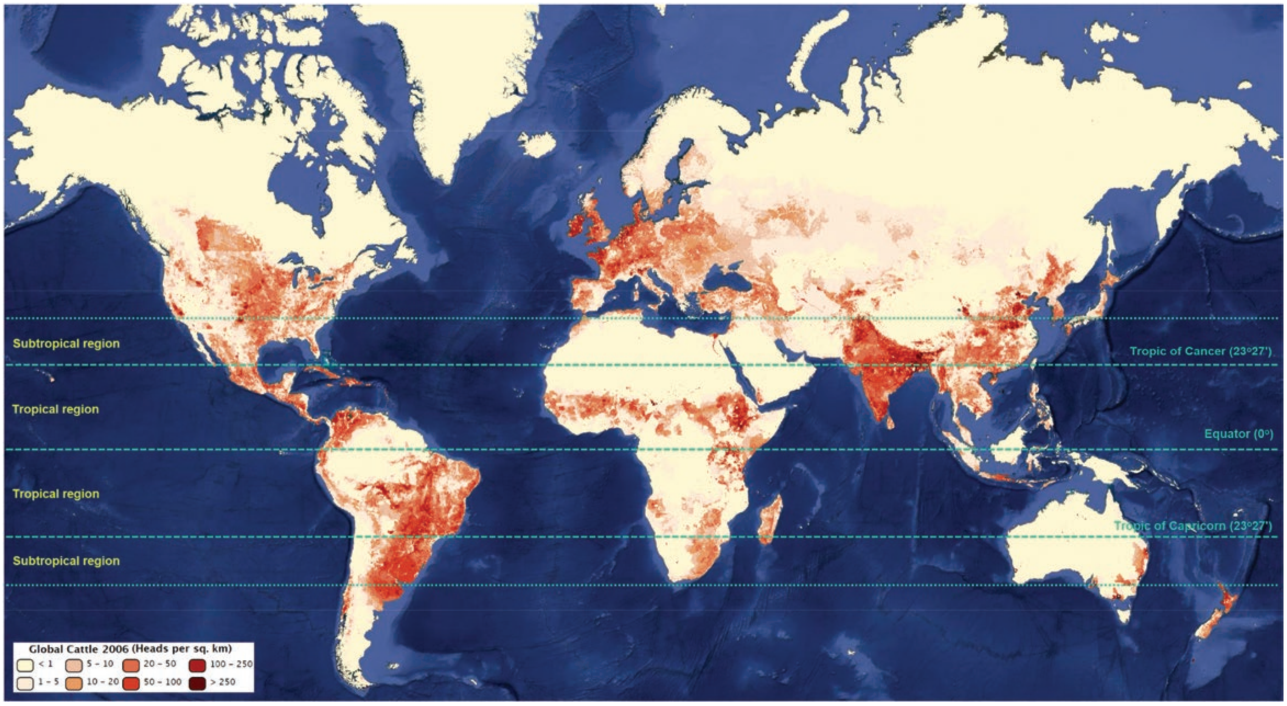

Figure 1. Distribution of cattle around the world in 2006 using the Gridded Livestock of the World 2 global distribution (https://application.geo-wiki.org/Application/index.php), based on Robinson et al. (2014). The position of the dashed lines for the tropic of Cancer (23°27′N), equator (0°), tropic of Capricorn (23°27′S), and the dotted lines delimiting the subtropical regions are a visual approximation and depicted for illustrative purposes only.

Table 1. Comparison between *Bos indicus* and *B. taurus* morphology, physiology, and behavior

Characteristic	*B. indicus*	*B. taurus*	Reference
Physical morphology			
Thoracic cavity length	Shorter	Longer	Swett et al. (1961)
Heart, omasum, abomasum, lung, liver, spleen, pancreas, pituitary, thyroid, and adrenal weight	Lighter	Heavier	Swett et al. (1961)
Size of reproductive tract and ovaries at mature luteal phase	Smaller	Larger	Adeyemo and Heath (1980)
Intestinal length	Shorter	Longer	Swett et al. (1961)
Skull length	Longer	Shorter	Clutton-Brock and Museum (1999)
Skull width	Narrower	Wider	Clutton-Brock and Museum (1999)
Dewlap	Present	Absent	Clutton-Brock and Museum (1999)
Ear and leg length	Longer	Shorter	Clutton-Brock and Museum (1999)
Hip height at 7-mo-old weaning	Taller	Shorter	Sanders et al. (2005); Riley et al. (2007)
Neural spines of posterior thoracic vertebrae	Bifurcated	Not-bifurcated	Clutton-Brock and Museum (1999)
Cervicothoracic or thoracic humps	Present	Absent	Sanders (1980)
Sweat gland size	Larger	Smaller	Nay and Hayman (1956); Pan (1963)
Sweat gland location relative to skin surface	Closer	Farther	Dowling (1955)
Behavior			
Phenotypic cohesiveness of groups	Tighter	Looser	Murphey (1990); Murphey and de Moura Duarte (1990)
Grazing duration	Longer	Shorter	Rhoad (1938); Bonsma and Le Roux (1953); Harker et al. (1954)
Distance traveled while grazing	Longer	Shorter	Rhoad (1938); Bonsma and Le Roux (1953)
Severity of offspring protective behavior	Stronger	Weaker	Costa et al. (2019)
Frequency of mounting surrounding estrus	Lower	Higher	Solano et al. (2005)
Growth and nutrition			
Longevity	Longer	Shorter	Chenoweth (1994)
Average daily gain until weaning	Greater	Lesser	Riley et al. (2007)
Body condition score at weaning	Greater	Lesser	Riley et al. (2007)
Average daily gain in the feedlot	Lesser	Greater	Cooke (2014)
Voluntary feed intake	Lesser	Greater	Rogerson et al. (1968); Frisch and Vercoe (1977b, 1978, 1984)
Maintenance requirements	Lesser	Greater	Frisch and Vercoe (1977b, 1978, 1984)
Feed efficiency on high roughage diet	Greater	Lesser	Frisch and Vercoe (1977a)
Water intake relative to increases in DMI and ambient temperature	Lesser	Greater	Winchester and Morris (1956)
Feed intake during sustained hot conditions	Unchanged	Reduced	Kibler and Brody (1951); Johnston et al. (1958); Allen (1962); Seif et al. (1979); Beatty et al. (2006)
Physiology and health			
Susceptibility to heat stress	Lesser	Greater	Adeyemo et al. (1979); Seif et al. (1979); Beatty et al. (2006); Eberhardt et al. (2009)
Resistance to ticks, worms, pinkeye	Greater	Lesser	Riek (1962); Strother et al. (1974); Frisch and Vercoe (1977b, 1978); Rechav (1987)
Mosquito attack tolerance	Greater	Lesser	Steelman et al. (1973, 1976)
Red blood cell counts and total cell volume	Greater	Lesser	Howes et al. (1963)
Hemoglobin values	Greater	Lesser	Howes et al. (1963)
Plasma cortisol in response to ACTH challenge	Greater	Lesser	Zavy et al. (1992)
Acute-phase response to weaning and transportation	Lesser	Greater	Qiu et al. (2007)
Change in heart rate as core internal temperature rises	Unchanged	Decrease	Beatty et al. (2006)
Ability to regulate body temperatures in hot environments	Greater	Lesser	Hansen (2004)
Internal heat production	Lesser	Greater	Seif et al. (1979)
Basal metabolic rate	Lesser	greater	Hansen (2004)

Behavioral and welfare implications

As the global climate changes, humans must reevaluate management decisions regarding which animals to use for food production. Part of promoting the sustainability of protein production and the beef industry itself is identifying animals that are best suited to current conditions and optimizing the housing, husbandry, and genetics utilized for health, growth, and behavioral needs. Because humans can dictate what type, where, and how animals are raised, more emphasis must be placed in identifying animals that are optimized for current environmental conditions, and these changes may differ drastically from historical practices.

Bos taurus and *B. indicus* are different subspecies of cattle

The evolution of cattle is a complex and dynamic phenomenon resulting from animal domestication, human migration from the Fertile Crescent, and environmental pressures. Based on mitochondrial DNA and fossil evidence, the Indian auroch (*B. primigenius namadicus*) diverged from Bison (*Bison bison*) approximately 1 million years ago (Figure 2; MacHugh et al., 1997). Approximately 300,000 years ago, the Indian zebu (*B. indicus*) diverged from the Eurasian auroch (*B. primigenius primigenius*). The Indian zebu represents today's modern Indian zebu breed (Loftus et al., 1994). The Eurasian auroch subsequently diverged into the African zebu (*B. primigenius indicus*), European taurus (*B. taurus taurus*), and African taurus (*B. taurus africanus*). As humans began to populate the planet, the cattle that accompanied them on their journey had to adapt to current environmental conditions. Those who survived the associated environmental stochasticity were the ones that were subsequently selected for domestication. Environmental pressures (e.g., local predators, climate, biome) dictated which individual cattle were successful in terms of survival rates (ability to find resources and avoid predators), thriftiness (efficiency in current biome forage availability), adaptability (capacity to change with the environment), and productivity. Consequently, cattle diverged into subspecies that differed in physiology, nutritional requirements, social behavior, and body composition (Table 1).

The cattle that were best suited for production in their current environment differed at the biome level. These external pressures have influenced the behavior and physiology of *B. indicus* cattle that are observed in contemporary animals. The geographical locations and accompanying biomes in which humans migrated and settled with *B. indicus* consisted of harsh conditions in which plants had relatively low nutritive value. These biomes also had a high prevalence of internal and external parasites, and predators that employed "stalk and surprise" hunting strategies. Accordingly, *B. indicus* cattle were typically found in environments with elevated environmental temperatures and dense foliage, which limited the field of view that they have to surveil for predators. These factors led to the evolution of cattle that graze in sinuous patterns (causing them to be more nutritionally efficient with low-quality forages), as well as those that are vigilant (Lima, 1998), more resistant to internal and external parasites (Strother et al., 1974; Frisch and Vercoe, 1977b), and quicker to respond to environmental stimuli (Costa et al., 2019).

Local predator hunting strategies also influenced prey behavior and stress responsivity (Miller et al., 2014). Cattle adapted to environments in which predators employ the "stalk and surprise" hunting strategy are more temperamental, have stronger activation of the sympathoadrenal system (Adeyemo et al., 1979), are more vigilant and more gregarious (Rhoad, 1938; Murphey, 1990; Lima, 1998), and may be more sensitive to interaction with humans (Lima, 1998). This is in contrast to cattle adapted to environments in which predators employee the "strategy and endurance" hunting strategy. Efficient cows had to alter their calf defense strategy accordingly. Cows defending against "strategy and endurance" predators benefit from having a sustained less-reactive prey response, as they are successful by judiciously using resources across time. Cows defending against "stalk and surprise" predators benefit from having an intense short-term predator response, or a long flight initiation distance. If these cows can survive the initial attack, they will have time to recover as repeated attacks by the same predator are rare and not in the predator's best interest (Brown et al., 1999). Therefore, these two types of animals have different thresholds for what will elicit an aggressive maternal response. Selection for cows that differ in their mothering approach is expected to differ physiologically, as their behavior to similar types of stimuli differs (Costa et al., 2019).

Ecological disruptions influence the biological functioning component of animal welfare

The planet's environment is changing at the same time as the global demand for high-quality protein continues to

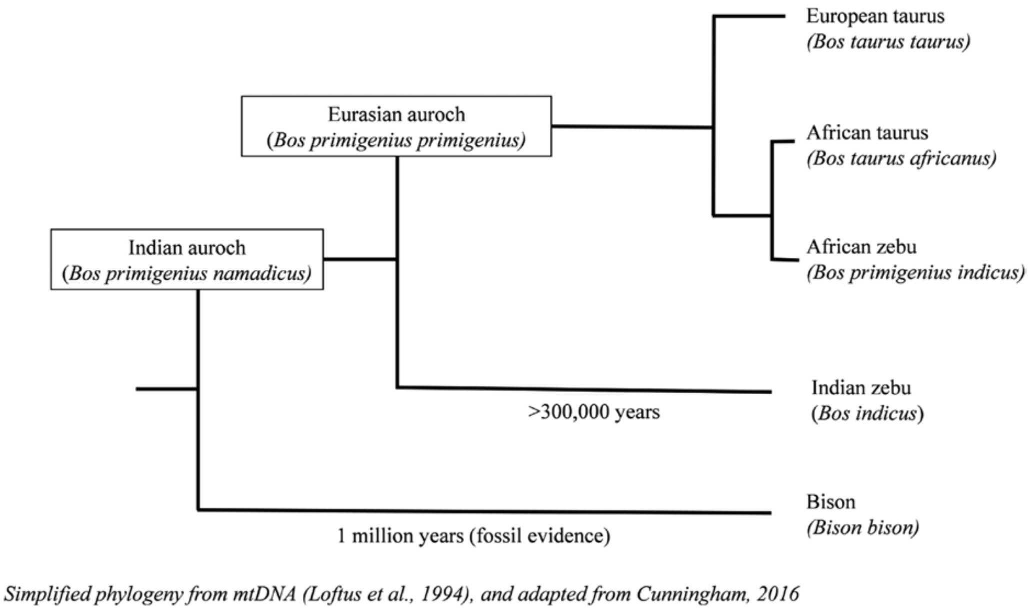

Figure 2. Simplified cattle phylogenetic tree based on Loftus et al. (1994).

increase, creating a scenario of compounding challenges that exacerbate the difficulties associated with efforts to feed the future (Hatfield et al., 2014). A fundamental step in meeting the increasing global demand for protein while addressing the environmental stewardship derived from climate change is to identify management practices optimized for the animals in our care. Contemporary cattle management does not necessarily require a complimentary relationship between cattle and the environment due to human-controlled breeding and transportation (Shetty, 2011; Polsky and von Keyserlingk, 2017; Yang et al., 2019). Yet, there are species-specific considerations to include when making breeding and relocation decisions. *Bos taurus* are more susceptible to heat stress (Table 1), while *B. indicus* are more susceptible to cold stress (Godfrey et al., 1991; Josey et al., 1993). Therefore, *B. indicus*-influenced cattle born and reared in subtropical and tropical regions of the planet will need different management (e.g., cold stress vs. heat stress mitigation) strategies while housed in the U.S. high plains during the finishing phase of beef production compared with *B. taurus,* which are more adapted and better equipped to cope with that environment. This dynamic between cattle genetics, weather, and commerce presents a scenario in which managers are actively engaged in proactive and reactive species-specific management strategies that facilitate coping in a stochastic environment (Busby and Loy, 1997; Brown-Brandl et al., 2013; Sjeklocha, 2018)

Consequences from the increasingly frequent and intense disruptive weather patterns (NOAA, 2019) have highlighted that different types of cattle respond differently to extreme weather events. As the weather patterns change, the environmental stress placed on cattle will change accordingly, thus cattle with the biological capacity to cope with these changes may experience better welfare. Rising environmental temperatures present one of the greatest threats to cattle welfare. As temperatures rise, *B. taurus* cattle will have to work harder than *B. indicus* cattle to thermoregulate and will be more susceptible to heat stress. Therefore, the need to use more *B. indicus*-influenced cattle in response to environmental pressures emphasizes the need to better understand species-specific needs. The differences in thermoregulatory capacities, behavioral reactivity, and nutritional efficiency (Table 1) between the two subspecies suggest that animal managers need to incorporate species-specific management strategies into daily husbandry practices. These strategies may include making environmental modifications (e.g., shade, mounds, bedding, environmental enrichment), exploring alternative pen riding strategies (e.g., frequency and timing of assessment, consistency of rider, integration of computer vision and body-mounted technology, interpretation of behavior, and sensor output), or altering purchasing decisions to ensure that animals within a single facility are able to equally cope with local conditions (Lees et al., 2019).

Bos indicus cattle are more gregarious than *B. taurus* and have more excitable temperaments; thus, they are more susceptible to social stress (Cooke et al., 2014). Moreover, *B. indicus*-influenced cattle may be more adept at masking injury and disease because more bold/excitable animals have a stronger antipredator response (Sih et al., 2004; Sih et al., 2012; Belgrad and Griffen, 2016); granted, this varies based upon the individual animal's previous experience and exposure to humans. Nevertheless, bovine respiratory disease (**BRD**), lameness, and bulling are three welfare and productivity issues that require behavioral evaluation to identify and treat. In general, accurate BRD detection rates are low, lameness is underreported by producers, and bulling continues to be one of the top welfare concerns for feedlot cattle (USDA, 2011; Timsit et al., 2016; Sadiq et al., 2019). Due to their more excitable temperament, *B. indicus* cattle may take longer to habituation to a new environment. However, taking the time to develop a positive human–animal relationship with *B. indicus* cattle may be worth the additional effort. Habituating cattle to humans may reduce the strength of the antipredator response, and as a consequence, their behavior may more accurately represent their internal state (Cooke, 2014). Therefore, implementing habituation strategies designed for cattle from different backgrounds and characterizing species-specific behaviors indicative of disease, injury and distress can have substantial economic and welfare implications.

Cattle behavior is influenced by the predator–prey dynamic, early and initial experiences can have lasting effects, and *B. indicus* cattle exhibit a strong antipredator response (Cooke, 2014). Emphasis must be placed on facilitating a positive human–animal relationship throughout the beef supply, particularly with *B. indicus* cattle. The valence and intensity of the predator–prey dynamic between handler and cattle can influence animal behavior toward handler and worker satisfaction, which are both important components of effective disease detection and can influence productivity (Schwartzkopf-Genswein et al., 1997; Lanier et al., 2000). Promoting a positive relationship between cattle and handler at the ranch and understanding the species-specific behavioral indicators of discomfort may facilitate early disease detection at the feedyard, thus contributing to the overall sustainability all while minimizing fear and stress (Hemsworth and Coleman, 2010).

Bos indicus cattle display different social behaviors compared with *B. taurus* counterparts, which may contribute to differences in production efficiency and outcomes. Besides mounting as a behavioral indicator of estrus, *B. indicus* cattle also perform headbutting (Solano et al., 2005), and this species-specific behavioral difference may have been influenced by what behaviors were evolutionarily important regarding mate acquisition and reproductive signaling in the wild. For example, mounting to indicate estrus while in a dense foliage is not a behaviorally efficient use of resources for *B. indicus*. One of the goals of mounting is to signal reproductive status and to attract the most qualified mate (Parker et al., 1976). In an open landscape, mounting is a visual signal in which information can be transferred a long distance, thus increasing the likelihood of attracting a suitable mate. When grazing in a landscape of dense foliage, the distance that the visual information from mounting can transfer is limited. Therefore, it is in the animal's best interest to use a secondary signal (e.g., sound or activity due to headbutting) to increase the number of potential mates that are alerted to her reproductive status. *Bos indicus* are typically found in biomes of denser foliage, thus they may need to engage in different behaviors than *B. taurus* to communicate the same information due to different environmental conditions. Engaging in headbutting in dense foliage generates noise, thus diversifying the type and widening the radius of communication in an effort to attract the best mate. Further, in *B. indicus* cows, the more dominant cows were more likely to perform mounting behavior, suggesting that social status may be regulated through mounting behavior, that social status may influence which cows behaviorally signal their physiological readiness for mating (Galina et al., 1996), and that similar behaviors may have different meanings across the different subspecies.

Understanding the social aspects of cattle adapted to tropical and subtropical enviroments, along with characterizing their biological thresholds regarding thermoregulation, disease resistance, transportation resiliency, and the human–animal interaction, will provide foundational data for developing appropriate stewardship practices. Predictive models show that the U.S. high plains will see an increase in heat waves through 2070 (Sarkis, 2018). Therefore, regions in the United States and across the globe that have historically been favorable for housing *B. taurus* cattle may need to alter their purchasing, breeding, and management strategies to ensure that irrespective of environmental conditions, genetics, and individual ontogeny, cattle are equipped with the tools to cope while maintaining productivity.

Warm-season perennial forage management

Forage availability played a critical role in the differentiation of *B. indicus* and *B. taurus* cattle and their subsequent adaptation to their environments, and still determines the productivity of beef production systems across the globe. Warm-season perennial grasses are the dominant forages used by tropically adapted cattle in tropical and subtropical regions; hence, understanding their characteristics to develop optimal forage management is imperative for beef cattle production in these areas. Most of the warm-season perennial grasses worldwide are native from Africa and were naturally selected for persistence under grazing, fire, and drought throughout the many years of existence in the African continent. Although warm-season perennial grasses are found up to latitude 53°′N, they have a greater presence between the tropics of Capricorn and Cancer. The carbon fixation pathway in C4 grasses allows these plants to be more adapted to warm and dry regions (Volenec and Nelson, 2007), commonly found in tropical regions. In addition, increasing atmospheric temperatures may favor the dominance of C4 species in different ecosystems. Cerling et al. (1993) used the C isotopic methodology to observe a worldwide expansion of C4 species and displacement of C3 vegetation. Some successful examples of productive warm-season perennial grasses in tropical and subtropical regions are the brachiaria grasses (*Brachiaria* spp.) in Brazil (Miles et al., 2004), buffelgrass (*Pennisetum ciliare*) in Australia (Loch, 1999), and bermudagrass (*Cynodon* spp.) in the southeastern United States (Taliaferro et al., 2004).

The resilience under adverse conditions is one of the most important characteristics of C4 grasses and is attributed to a combination of morphological and physiological mechanisms. The most commonly used C4 species in subtropical regions can allocate photosynthates between reserve structures, and store C and N that can be remobilized after grazing (Moore et al., 2004). Although some C4 grass species can store a substantial amount of their reserves below ground, management practices can also impact their root-rhizome mass and nutrient content. Liu et al. (2011) observed that total nonstructural carbohydrates mass decreased from 30.6 to 26.5 g/m^2 in "Tifton 85" bermudagrass plants grazed from 24- to 8-cm stubble height. Vendramini et al. (2013) tested different bahiagrass (*Paspalum notatum*) cultivars defoliated at different frequencies (2 or 4 wk interval), and found that "Argentine" bahiagrass had greater root-rhizoma mass than Tifton 9 and the UF-Riata when harvested every 2 wk; however, there were no differences in root-rhizome mass on plants harvested every 4 wk. Consequently, "Argentine" bahiagrass had greater ground cover than the other cultivars at the end of the experimental period and demonstrated greater persistence under frequent defoliation. The most resilient C4 grasses also have morphological adaptations that protect their meristematic zones (Crawley, 1997). The phenotypic plasticity reflects the ability of an individual plant to change morphologically or physiologically in response to climate or management stress (Baron and Belanger, 2007). According to Richards and Caldwell (1985), the location, number, and activity of meristems remaining on the defoliated plant and morphological plasticity may be more important in the long-term process of regrowing the leaf area.

Despite the vast dominance of C4 grasses in tropical and subtropical climates, warm-season legumes (C3) have also been used within these regions. The increased cost of N fertilizer has led to significant efforts to develop warm-season legumes that can be used to reduce the dependency on commercial N fertilizer in grazing systems. In general, warm-season legumes have greater nutritive value than C4 grasses and can fix atmospheric N, adding nitrogen to the grazing system. The N is transferred from legumes through exudation and leakage of N from roots and nodules, senescence and degradation of nodules and roots, direct transfer from legume roots to nonlegume roots through connections made by arbuscular mycorrhizal fungal hyphae, movement of N from legume herbage to the soil by leaching or decomposition of surface litter, and redeposition of consumed N by livestock. However, the predominant pathways are the decomposition of above- and below-ground plant residues and return of N via animal excreta (Vendramini et al., 2014). The widespread use of warm-season legumes has been limited because of decreased persistence under grazing, limited competitiveness with warm-season grasses, and high incidence of diseases (Muir et al., 2011).

Forage nutritive value and quality

The terms nutritive value and quality have been used interchangeably in the forage literature; however, they are distinct entities. Nutritive value is defined as "the chemical composition, digestibility, and nature of the digested products of forage, commonly expressed as a proportion of the total." Forage quality is expressed as "animal product and is measured when forage quantity and animal genetic potential are not limiting, and forage is the sole source of energy and protein" (Moore, 1994).

The differences in C4 grass species along with the effects of management practices make it difficult to accurately estimate energy concentration in C4 plants. Cell walls (neutral detergent fiber [NDF]) and their derivatives (acid detergent fiber [ADF]) have been used either alone or with other chemical entities to predict both intake and digestibility (Moore et al., 1996). ADF is frequently used by feed testing laboratories to estimate digestibility. Reported coefficients of correlation between concentrations of ADF and digestibility of organic matter (OM) and dry matter (DM) vary from −0.50 to −0.95 (Minson, 1982). According to Moore and Undersander (2002), published correlation coefficients have ranged from −0.39 to −0.93 between digestible DM and ADF. Greater coefficients of correlation between ADF and digestibility are generally found in cool-season forages or total mixed ration (**TMR**) but not in C4 grasses. In vitro procedures have been widely used to estimate C4 grasses digestibility because it measures two nutritive entities: cell contents and digestible cell walls. These procedures are considered precise methods and are capable of analyzing multiple samples at the same time. In addition, many studies have shown a strong correlation between in vivo and in vitro digestibility data (Weiss, 1994).

Forage quality is a function of nutritive value and intake. According to Mertens (2009), forage quality is affected by intake (50% to 70%), digestibility (24% to 40%), and metabolism (5% to 15%). Mertens (1987) proposed that daily NDF intake in dairy cattle was 1.20% of body weight (BW) per day in diets that produced maximum daily 4% fat-corrected milk. However, this concept is limited because NDF is a poor predictor of intake across many forage types, particularly C4 perennial grasses (Moore and Undersander, 2002). The DM intake is not well correlated with NDF concentration across a variety of warm-season forages (Moore and Undersander, 2002). Because of the complexity associated with forage composition, structure, degradation, and voluntary intake control, it is unrealistic to expect that one single measurement of nutritive value will be a universal predictor of intake (Moore, 1994). Forage selectivity and difference in BW between animal subspecies, breeds, category, physiological state, and several other aspects also render the prediction of DM intake based on NDF (Mertens, 1987) inadequate for beef cattle (Tedeschi and Fox, 2018; Tedeschi et al., 2019).

Hernandez-Garay et al. (2004) showed a quadratic relationship between average daily gain (ADG) of steers grazing stargrass pastures and herbage allowance (**HP**). Increasing average HP up to 4 kg DM/kg of BW resulted in a linear increase in ADG. As the average HP increased above 4 kg DM/kg BW, the rate of increase in ADG decelerated (Figure 3). In heifers grazing bahiagrass and "Mulato" brachiariagrass (*Brachiaria* spp.) pastures, Inyang et al. (2010) reported increased ADG as HP increased up to 1.4 kg DM/kg of BW, whereas ADG remained constant (≈0.28 kg/d) when HP was above 1.4 kg DM/kg of BW (Figure 3). The close relationship between HP and ADG corroborates that the major factor affecting cattle growth rate at a high stocking rate is herbage quantity. Greater HPs allow ruminants to maximize intake, which is the main factor affecting forage quality. However, the nutritive value may also impact forage quality and explain more than 50% of the variation in ADG when forage quantity is not limiting (Sollenberger and Vanzant, 2011).

When considering forage quality for ruminants grazing C4 grasses, several additional factors may affect DM intake. The vertical heterogeneity in sward canopy structure and composition and the amount and accessibility of leaf are major canopy characteristics associated with intake. Green herbage mass or green leaf proportion in grazed horizon usually shows positive relationship with bite weight, and forage intake is a function of bite weight and bite rate (Burns and Sollenberger, 2002). Euclides et al. (1993) and Euclides et al. (2000) observed a positive correlation between green herbage mass, leaf mass, proportion of leaves, and forage DM intake in steers grazing brachiariagrass and guineagrass (*Panicum maximum*; Table 2). Leaf density, plant-part composition, and nutritive value of the upper canopy are also important to explain the variations in the intake. Although leaves of mature tillers maintain relatively high quantity despite reducing quality as they age, grazing animals often cannot maintain a high level of intake because of the wide spatial arrangement of the leaves on elongated tillers (Moser and Jenning, 2007). In turn, bite size and forage intake are maximized when the canopy is comprised of leaves on relatively tall and densely packed vegetative tillers (Moser and Jenning, 2007).

Nutritional considerations and recommendations

Changes in the weather pattern and production needs, as previously mentioned, may impact the geographical distribution of *B. indicus* and *B. taurus* cattle across the globe. As an example, *B. indicus*-influenced cattle dominated the tropical and subtropical regions in the mid-1950s, except for the Americas as descendants of early Spanish cattle still prevailed (Phillips, 1961). This trend began to change as *B. indicus* cattle displayed superior production traits under hot climates, where the majority of the global cattle population is located (Figure 1). Many factors complicate the nutritional management of cattle in tropical and subtropical regions. These include biological differences between *B. indicus and B. taurus* cattle, the reduced nutritive value of C4 forages as previously discussed, and increased energy requirement for maintenance due to heat stress and diseases. Hence, nutritional management of cattle raised in tropical and subtropical environments deserves special consideration and cannot rely on recommendations established for *B. taurus* cattle in temperate climates.

Energy requirement

Despite the predominance of *B. indicus* breeds, beef production in tropical and subtropical regions also contain *B. taurus* breeds. *Bos indicus* cattle are more tolerant to heat stress and ectoparasites (e.g., *Rhipicephalus* [*Boophilus*] *microplus*), but more susceptible to trypanosomosis (Hanotte et al., 2000; Rocha et al., 2019) compared with *B. taurus* counterparts. The direct adverse effects of ectoparasites on energy requirement are related to the additional energy expenditures associated with blood loss, incidence of anemia, depression of immune function, suppression of feed intake, increased stress, and increased physical activity

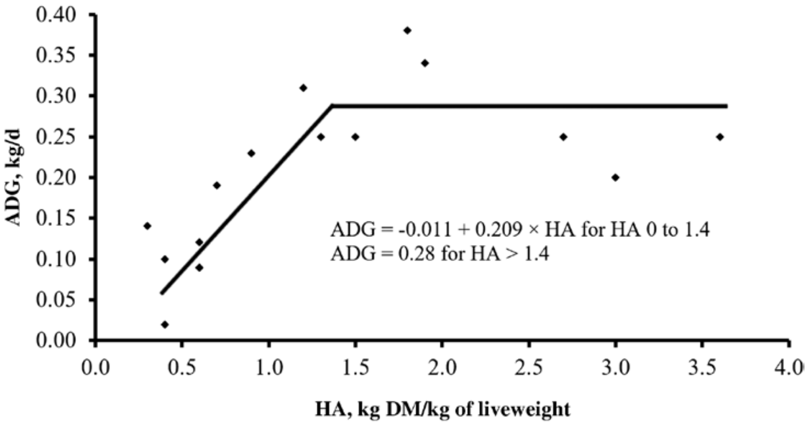

Figure 3. A nonlinear correlation between **HA** (kg dry matter/kg of liveweight) and ADG for Mulato and bahiagrass pastures stocked at 4, 8, and 12 heifers/ha (Inyang et al., 2010).

Table 2. Correlation coefficients between canopy attribute and forage dry matter intake in brachiariagrass (*Brachiaria* spp.) and guineagrass (*Panicum maximum*). Adapted from Euclides et al. (1993) and Euclides et al. (2000)

Canopy attribute	*Brachiaria* spp.	*Panicum maximum*
Green Herbage Mass	0.55–0.61	0.64
Leaf mass	0.51–0.59	0.60
Leaf %	0.46–0.65	—

in response to infestation (Jonsson, 2006). Thus, *B. indicus* and *B. taurus* animals may have different energy requirements brought about by the infestation with ectoparasites. Yet, *B. indicus* breeds have reduced growth rates under tropical and subtropical conditions, despite their tolerance to ectoparasites, compared with *B. taurus* under temperate standards. Frisch and Vercoe (1978) believed that a compromise could explain why *B. taurus* have greater performance compared with *B. indicus* under feedlot conditions but underperformed under drought and grazing conditions. Indeed, a metabolic compromise might exist so that the underperformance of *B. indicus* is related to their intrinsic ability to cope with environmental constraints found in tropical and subtropical regions, which limits their growth performance or carcass quality. This metabolic compromise may also explain the variations in energy requirement for maintenance reported in the literature. Assuming energy intake is not limiting, the energy requirement for growth is a direct function of body chemical composition and thus less prone to variations in environmental conditions.

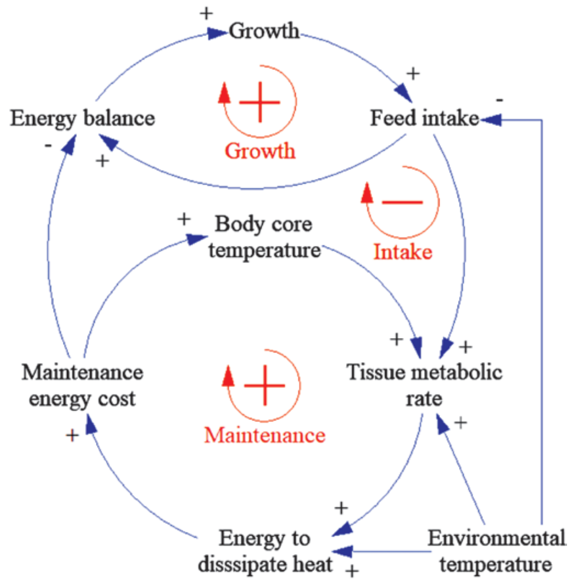

Figure 4. Conceptual relationship showing three feedback loops (maintenance, growth, intake) of energy partitioning of animals under heat-stressed conditions. The self-reinforcing and self-correcting loops are represented by the positive and negative signs, respectively, with the semicircle arrows. Positive and negative signs at the arrowheads indicate the effect is positively or negatively related to the cause, respectively.

Heat stress

Hot and humid environments are known to induce heat stress and decrease productive and reproductive efficiencies of livestock (Fuquay, 1981). As depicted in Figure 4, environmental temperature affects animal productivity in two ways. The first way is a direct effect on the feed intake, as feed intake decreases when the temperature is above the stage 4 of the upper critical limit (Beede and Collier, 1986; NASEM, 2016; Tedeschi and Fox, 2018). However, reduced feed intake only accounts for 30% of production losses due to heat stress (Rhoads et al., 2010). The second and the most likely, more impactful way is through animal metabolism. Elevated environmental temperatures increase tissue metabolism and the amount of energy needed to engage in thermoregulation (e.g., sweating and panting), which in turn increases maintenance energy requirements, leading to increase body core temperature that further increases tissue metabolism (NASEM, 2016). The meticulous coordination among the feedback loops (maintenance, growth, and intake) reported in Figure 4 is essential to achieve homeostatic body core temperature. The greater tolerance for heat stress by *B. indicus* breeds compared with *B. taurus* has been extensively documented (Gaughan et al., 2008). In fact, *B. indicus* breeds have a lower resistance of body tissues to transfer metabolic heat to the skin compared with *B. taurus* breeds (Finch, 1986). This physiological adaptation might have resulted from an evolutionary event that conferred, at least in part, *B. indicus* breeds to have less marbling scores compared with *B. taurus*. Accordingly, inter- and intra-muscular fat depots would insulate the animals and impair the dissipation of heat generated by the metabolic processes. Despite the historical importance of heat stress on cattle productivity and the development of several nutritional and mathematical models since the mid-1970s, the National Research Council has adopted simple adjustment factors (often based on the panting score) to account for heat stress on energy requirements for maintenance (Tedeschi and Fox, 2018). Simulations of such adjustments have indicated that the impact of heat stress on DM intake would be more severe when night cooling (i.e., night temperature below 20 °C) does not occur. For lactating dairy cows, simulations in milk production indicated that the milk reduction is four times greater for scenarios without night cooling compared with scenarios with night cooling (Tedeschi and Fox, 2018), whereas high-producing dairy cows are usually more susceptible to heat stress than low-producing counterparts (Carabaño et al., 2016). Therefore, comprehensive mechanistic models based on heat and mass transfer relationships are still needed to improve cattle performance in tropical and subtropical environments (DeShazer, 2009).

Energy required for maintenance

Since the publication of the California Net Energy System by Lofgreen and Garrett (1968) to determine energy requirements for growing cattle, the establishment of the requirement of net energy for maintenance (NEm) of *B. indicus* breeds has been a subject of much interest and debate. In part, the inconsistencies might be due to environmental adaptability associated with the tolerance to heat stress (e.g., the resistance to transfer metabolic heat), as well as the difficulties in determining retained energy through the comparative slaughter technique (Tedeschi et al., 2017; Tedeschi, 2019). Recently, comprehensive discussions have been provided by the NASEM (2016) and Tedeschi and Fox (2018) on the NEm requirement for *B. indicus* breeds. Some studies have reported that *B. indicus* breeds have greater NEm requirements than *B. taurus* breeds, others have reported no differences, and some have reported that *B. indicus* breeds have lower NEm requirements than *B. taurus* (Tedeschi and Fox, 2018). Besides genetic differences among breeds within subspecies and the genetic selection imposed on the breeds over the years, different methodologies and techniques might have contributed to the discrepancy in the results. These include shrunk vs. empty BW, linear vs. nonlinear regressions, variable multicollinearity, and assumptions about physical activities.

Figure 5 illustrates the impact of different methodologies and techniques on the estimates of NEm requirement. The database used for *B. taurus* (n = 31) was that listed by Lofgreen and Garrett (1968), except that metabolizable energy intake (**MEI**) and heat production (**HP**) were scaled to empty BW (EBW) basis, and assuming the reported metabolic weight was on shrunk BW (**SBW**) basis (Tedeschi and Fox, 2018) with a fixed EBW:SBW ratio of 0.891 adopted for interconversion (NASEM, 2016). The database used for *B. indicus* (n = 566) was developed by Marcondes et al. (2013), containing purebreds and crossbreds of Nelore heifers, steers, and bulls. A Monte Carlo simulation (n = 5,000) was developed using the mean and standard error (i.e., standard deviation) of the parameter estimates, more specifically the intercept estimates. When expressed on EBW basis and using a linear regression of the logarithm of the HP (kcal/kg$^{0.75}$) on the MEI (kcal/kg$^{0.75}$), the NEm estimates (kcal/kg$^{0.75}$) between *B. indicus* (74.93 ± 1.019) and *B. taurus* (84.59 ± 1.041) did not overlap and *B. indicus* had 11.4% less NEm required than *B. taurus* (Figure 5A). Conversely, when using an exponential regression of the HP (kcal/kg$^{0.75}$) on the MEI (kcal/kg$^{0.75}$), the NEm estimates (kcal/kg$^{0.75}$) between *B. indicus* (79.29 ± 1.566) and *B. taurus* (86.56 ± 4.038) overlapped by 18%, and *B. indicus* had only 6.3% less NEm required than *B. taurus* (Figure 5B).

Linear regression of the logarithmic transformation of HP has been used in the past because its estimate of 77 kcal/kg$^{0.75}$ of SBW by Lofgreen and Garrett (1968) was similar to the 70 kcal/kg$^{0.75}$ reported by Kleiber (1947), whereas the existence of applied nonlinear regression algorithms in the 1960s was also scant. Besides other known regression hurdles (e.g., variable multicollinearity; Koong, 1977), the use of logarithmic transformation instead of nonlinear regression might be objectionable nowadays. Moreover, recent genetic advances in Nelore cattle for postweaning growth changed the physical and chemical characteristics of their carcasses, which likely altered their energy requirement (Bonilha et al., 2008; Bonilha et al., 2011). Thus, the determination of a single coefficient to estimate energy requirements to a specific breed will probably yield incorrect recommendations, let alone the discrepancies brought about by different methodologies and techniques to generate such coefficients.

Considerations on fiber digestibility and inclusion

The adoption of managerial and feeding strategies to assist animal performance in the tropical and subtropical regions is critical to achieving efficient production. More energy-dense diets may be an alternative as intake is usually reduced under heat stress conditions (Beede and Collier, 1986). However, appropriate dietary fiber is still needed to maintain adequate rumen health, whereas DM intake tends to increase as NDF provided by dietary forage increases (Galyean and Defoor, 2003). Since the mid-1940s, it has also been shown that fiber has a lower impact on OM digestibility in *B. indicus* breeds than *B. taurus* breeds (Duckworth, 1946), suggesting that DM digestibility is slightly greater for *B. indicus* than *B. taurus* when dietary fiber levels are elevated (Warwick and Cobb, 1976). Assuming that an ideal ruminal pH to maximize the fractional degradation of fiber is around 6.6 (Mouriño et al., 2001), and using equation 1 (Fox et al., 2004; Tedeschi and Fox, 2018) to compute the optimum of physically effective NDF (**peNDF**) and equation 2 (Jennings et al., 2019) to compute the rumination time given the peNDF, we obtained an ideal peNDF of 27.78% DM and that growing cattle should ruminate at least 410 min/d to maintain a healthy ruminal pH. The estimated ideal peNDF is greater than the

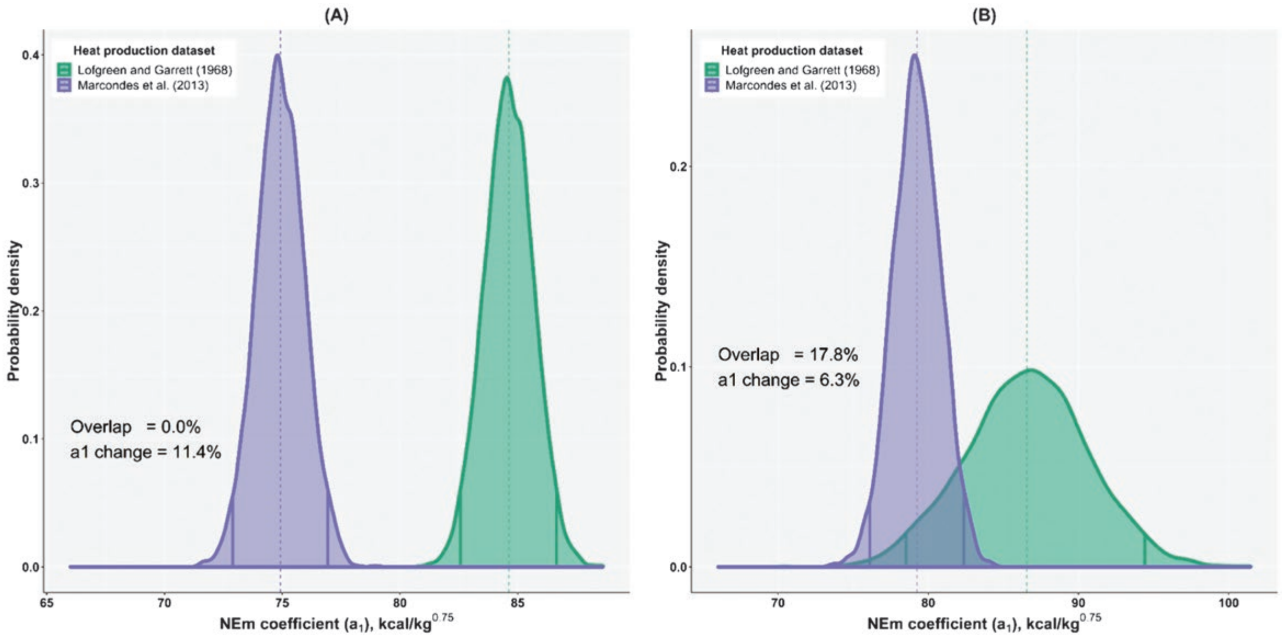

Figure 5. Probability density functions (**PDF**) based on Monte Carlo simulation assuming a normal distribution of the coefficients of the NEm of *Bos taurus* [green; dataset developed by Lofgreen and Garrett (1968)] and *B. indicus* cattle [purple; dataset developed by Marcondes et al. (2013)]. Panel A used a linear regression of the logarithm of daily HP per metabolic EWB (kcal/kg$^{0.75}$) on daily MEI per metabolic EBW (kcal/kg$^{0.75}$), and the estimates were 74.93 ± 1.019 and 84.59 ± 1.041 kcal/kg$^{0.75}$ (P = 0.0099) for *B. indicus* and *B. taurus*, respectively. Panel B used an exponential regression of daily HP per metabolic EWB (kcal/kg$^{0.75}$) on daily MEI per metabolic EBW (kcal/kg$^{0.75}$), and the estimates were 79.29 ± 1.566 and 86.56 ± 4.038 kcal/kg$^{0.75}$ (P = 0.0978) for *B. indicus* and *B. taurus*, respectively. The dashed vertical lines represent the averages, and the solid vertical lines represent the 95% quantiles of the PDF.

24.5% recommended by Fox et al. (2004) but less than the 31.2% reported by Zebeli et al. (2012). Assuming that rumination time is about 159 min/kg NDF (Jennings et al., 2019), an animal would have to consume at least 2.58 kg NDF/d to obtain 410 min per day. For an 80% NDF forage, animals would need to consume about 3.2 kg/d of the forage. For a 50% NDF forage, animals would need to consume about 5.16 kg/d of the forage and so on. For forages with higher digestibility (low NDF content), the peNDF would probably be less than the feedstuffs used to develop equation 2 (corn stalks), thus quickly requiring animals to consume more forage than they can handle and still be productive.

$$pH = 5.425 + 0.04229 \times peNDF \tag{1}$$

$$peNDF = 0.0008 \times RT - 0.0505 \tag{2}$$

Where *NDF* is neutral detergent fiber, kg/d; *peNDF* is physically effective NDF, % DM; *pH* is ruminal pH; and *RT* is rumination time, h/d.

Although equations 1 and 2 were largely developed using *B. taurus* breeds, they illustrate the relationship between rumination time and ruminal pH. Under certain conditions, the mean ruminal retention time for *B. indicus* might be shorter than for *B. taurus* (Hungate et al., 1960; Phillips et al., 1960), suggesting the fractional degradation rate of the fiber has to be faster so that the OM and DM digestibilities can be greater in *B. indicus* than in *B. taurus,* as discussed above. In part, differences in ruminal digestibility might be due to feed selectivity and particle size. Therefore, rumination time and ruminal pH might be slightly different for *B. indicus* breeds compared with those represented by Equations [1] and [2], but their interdependency still exists.

Nevertheless, as depicted in Figure 4, lowering heat increment and tissue metabolism seems desirable for heat-stressed cattle. However, fiber (i.e., NDF) fermentation produces more heat than concentrate (i.e., grain). Therefore, although fiber is needed to maintain rumen health (i.e., motility and pH), it may have a negative impact due to its greater heat of fermentation. In that sense, the least amount of NDF should be provided to cattle under heat stress conditions, and an increased proportion of dietary fat could be fed (Beede and Collier, 1986).

Other nutrients

Additional considerations have been done for supplemental protein, and mineral and vitamin balances to maintain acid–base homeostasis (Beede and Collier, 1986) in heat-stressed cattle. The metabolizable protein required by Nelore cattle (Rotta et al., 2016) is meagerly 5% greater than that recommended by the NASEM (2016) (4 vs. 3.8 g/kg$^{0.75}$ SBW, respectively). In the same token, the recommendations for Ca, P, Mg, Na, and K for Nelore cattle (Costa e Silva et al., 2016) are similar to those for *B. taurus* raised in temperate regions (NASEM, 2016). Nonetheless, research studies comparing protein, mineral, and vitamin requirements between *B. indicus* and *B. taurus* breeds are still limited, and thus warranted for the optimal nutritional management of cattle in tropical and subtropical conditions.

Novel nutritional concepts and strategies

Bos taurus and *B. indicus* cattle not only exhibit diet-dependent differences in intake, digestion, and ruminal fermentation (Hunter and Siebert, 1985a, 1985b; Habib et al., 2008; Bell et al., 2017) under the same environmental conditions, but also display differences in ovarian function, physiology (Sartori et al., 2016), and fetal growth (Mercadante et al., 2013; Fontes et al., 2019). These differences may determine the direction and magnitude of performance responses to similar management practices applied to *B. taurus* or *B. indicus* breeds. Therefore, nutritional interventions to enhance production responses need to be specifically tailored to *B. indicus*-influenced cattle in tropical or subtropical conditions. Examples of such interventions are described and discussed below.

Polyunsaturated fatty acids

Fat supplementation rich in linoleic and linolenic acids has been widely used due to its nutraceutical benefits to cattle reproduction (Staples, 1998; Cooke, 2018). Combining soybean oil with Ca salts (**CSSO**) is a strategy to minimize ruminal biohydrogenation (Sukhija and Palmquist, 1990) and increase tissue incorporation of linoleic acid (Cooke, 2018). Supplementing 100 g/d of CSSO after fixed-time artificial insemination (AI), increased pregnancy rates in Nelore cows grazing tropical forages compared with iso-caloric and iso-lipidic supplement based on saturated fat (Lopes et al., 2009, 2011), likely due to the enhanced conceptus development and *interferon-tau* synthesis during the pregnancy recognition period (Cipriano et al., 2016; Fricke et al., 2016). Pregnancy establishment and overall reproductive physiology differ between *B. indicus* and *B. taurus* females (Sartori et al., 2016; Fontes et al., 2019), but also the fatty acid composition between tropical and temperate feed ingredients. Despite those differences, supplementing 100 g/d of CSSO for 21 d after AI also increased pregnancy rates to fixed-time AI in *B. taurus* females (Brandão et al., 2018; Table 3). Thus, supplementing CSSO rich in linoleic acid can be implemented to increase the overall reproductive performance of *B. taurus* and *B. indicus* beef cows reared in tropical and subtropical environments (Cooke et al., 2019; Table 3).

Injectable trace minerals

In a series of three experiments, Arthington et al. (2014) evaluated the impacts of injectable trace minerals (**ITM**) on pre- and post-weaning performance of Brangus calves grazing warm-season grasses. Authors reported that: 1) preweaning BW gain did not differ between calves administered ITM or sterile saline injections at birth, 100, and 200 d of age, but ITM calves had increased liver concentrations of Cu and Se compared with saline calves; 2) ITM administration immediately after a 24-h transportation period not only increased the concentrations of plasma haptoglobin and liver Cu, Se, and Zn, but also decreased post-transportation ADG compared with saline injection (–0.27 vs. 0.14 kg/d, respectively); and 3) overall ADG, antibody titers following an immunological challenge with porcine red blood cells, and liver Se concentrations were greater for heifers receiving ITM vs. saline solution on days 0, 51, and 127 of a 177-d development period. Together, these results demonstrate that ITM may successfully increase trace mineral status, humoral immune response to novel antigen, and the acute-phase response after weaning- and transportation-induced stress in growing *B. indicus*-influenced calves.

Despite the variable responses, ITM has also been implemented to enhance the reproductive performance of beef cows. However, only one of four studies (Table 3) reported that a single ITM administration increased the pregnancy rates to fixed-time AI in *B. taurus* heifers (Stokes et al., 2017, 2018). Along with other potential reasons, cattle breed is one plausible reason for the discrepancy in the results described above, given that

Table 3. Pregnancy to AI of beef females supplemented or not with CSSO, and beef females administered saline solution or ITM

Item	Pregnancy rates, %	P-value
Cooke et al. (2019)[1]		
Control	38	< 0.01
CSSO	49	
Brandão et al. (2018)[2]		
Control	52	0.01
CSSO	60	
Stokes et al. (2017)[3]; exp.1		
Saline	65	≥ 0.74
TM	61	
Stokes et al. (2017)[3]; exp. 2		
Saline	45	0.07
ITM	62	
Stokes et al. (2017)[3]; exp. 3		
Saline	66	≥ 0.50
ITM	61	
Stokes et al. (2018)[4]		
Saline	30	0.36
ITM	37	
Vedovatto et al. (2019)[5]		
Cows with body condition score < 5		
Saline	47	0.09
ITM	58	
Cows with body condition score ≥ 5		
Saline	68	0.36
ITM	72	

[1] Nelore cows (n = 3,355) grazing tropical pastures and supplemented or not with 100 g/d (as-fed basis) of CSSO. Supplementation period ranged from d –11 to 28 relative to artificial insemination.
[2] Angus cows (n = 771) consuming temperate forages and supplemented or not with 100 g/d of CSSO for 21 d after fixed-time artificial insemination.
[3] Exp. 1 = Angus (n = 93); exp. 2 = Angus × Simmental (n = 120); exp. 3 = Angus (n = 199). Heifers were injected with saline injection or ITM (1 mL/68 kg BW) 33 d prior to breeding.
[4] Angus heifers (n = 290) were administered saline or ITM at 221 and 319 d of age (1 mL/45 kg BW) and at 401 and 521 d of age (1 mL/68 kg BW) and bred via AI at 430 d of age.
[5] Nelore cows (n = 573) administered saline or ITM (6 mL/cow) 30 d before AI.

breed type may affect the postinjection amount of circulating antioxidant enzymes produced and the storage time of trace minerals (Pogge et al., 2012). Vedovatto et al. (2019) evaluated the effects of a single ITM injection administered 30 d before AI on physiological responses of *B. indicus* cows grazing tropical low-quality forages. A single ITM injection had no effects on BW and body condition score (BCS) change, ovarian structures, and inflammatory responses, but increased plasma concentrations of antioxidant enzymes compared with saline solution injection. In addition, ITM injection improved pregnancy rates to AI in cows with BCS < 5 (85.4 vs. 46.8%, respectively), but not for those with BCS ≥ 5 (71.8 vs. 67.5%, respectively), suggesting that pre-breeding ITM may be a strategy to boost reproductive performance of beef cows reared in nutrient-limited conditions.

Nutritional management during gestation

Fontes et al. (2019) reported that pregnancy loss was greater for Angus vs. Brangus cows when these animals were fed an energy-restricted diet (70% of daily energy requirements), but did not differ between breed types when cows were offered 100% of their daily energy maintenance requirements. Furthermore, Mercadante et al. (2013) demonstrated that *B. taurus* fetuses were larger than *B. indicus* fetuses at days 53 to 62 of pregnancy, but not at earlier time points. *Bos indicus*-based breeds have extended gestation lengths and yield calves with similar or greater birth weights than *B. taurus* breeds (Riley et al., 2007; Mercadante et al., 2013), suggesting that *B. indicus* cattle may compensate for delayed fetal development by extending their gestation length. Together these data indicate that fetal development is mostly driven by fetal genotype, but also modulated by the maternal uterine environment (Ferrell, 1991; Mercadante et al., 2013).

An accruing amount of evidence has been published over the last decade supporting the concept of fetal programming impacting long-term performance of beef cattle. An in-depth review of fetal programming is not the goal of this section, given that few studies have explored the fetal programming concept in *B. indicus*-influenced cattle compared with *B. taurus* females. Nonetheless, limited research in *B. indicus*-influenced cattle is an opportunity for future research and warrants attention. As previously mentioned, breed determines the performance response to nutritional management and pattern of fetal growth. Hence, it is possible that, when exposed to similar gestational nutritional management, the existence and magnitude of fetal programming effects on postnatal offspring performance differ between *B. taurus* and *B. indicus* cows. Accordingly, most fetal programming studies in *B. taurus* cattle reported that supplemental nutrition during late gestation increased calf birth weight and preweaning growth performance (Bohnert et al., 2013; Marques et al., 2016). In *B. indicus*-influenced cattle, similar improvements in calf postnatal growth have not been reported in the majority of the studies investigating cow supplementation during gestation (Sullivan et al., 2009; Marquez et al., 2017; Nepomuceno et al., 2017).

Early weaning

The cow-based energy costs associated with raising a calf are important to the efficiency of a cow-calf production system. Early weaning (**EW**) is defined as separating their calves from their dams prior to 180 d of age (Rasby, 2007). Compared with normally weaning, EW calves of *B. indicus*-influenced primiparous cows resulted in a substantial reduction in the amount of the energy required to support the combined need for lactation and the continued growth of the dam (Arthington and Minton, 2004). Cows and their calves normally weaned at 8 to 9 mo of age consumed an average of 58% more DM and 59% more energy (from both hay and supplement) during a 10-wk study compared with EW cows (Arthington and Minton, 2004). However, this increase in nutritional status enhanced the reproductive performance of primiparous, but not multiparous cows. Primiparous cows whose calves were weaned at 3 mo of age had greater BW gain and BCS during the breeding season, decreased postpartum interval (Arthington and Minton, 2004), and increased pregnancy rates compared (94% vs. 65%, respectively) with cohorts whose calves were weaned at 8 mo of age (Arthington and Kalmbacher, 2003). Pregnancy rates did not differ between multiparous cows whose calves were weaned at 3 or 9 mo of age (92% and 93%, respectively). In fact, calving distribution was delayed in EW vs. normally weaned multiparous cows (Arthington and Vendramini, 2013). Therefore, EW is an effective management to increase the productivity of primiparous, but not multiparous beef cows in tropical and subtropical regions.

Similar benefits of early weaning were noted in *B. taurus* primiparous cows reared in temperament environments (Peterson et al., 1987; Story et al., 2000; Rasby, 2007), although feed availability and costs during winter largely determine the economic viability of early weaning (Merrill et al., 2008). In tropical and subtropical regions, mild winters offer an opportunity to raise calves on pasture systems using annual cool-season or perennial warm-season grasses. However, regardless of forage type, concentrate supplementation is necessary for EW calves to achieve desirable levels of gain on pasture. Early-weaned calves receiving 1.0% of BW of a supplement (15% crude protein [CP] and 70% total digestible nutrients [TDN]) or no supplementation gained 0.74 and 0.30 kg/d, respectively (Vendramini et al., 2006). In warm-season grazing systems, daily concentrate supplementation at 0%, 1.0%, 1.5%, and 2.0% of BW (DM basis) increased ADG from 0.42 to 0.65 kg/d, with supplementation at 1.5% of BW resulting in greater net return than EW calves supplemented at 1.0 and 2.0% of BW (Vendramini et al., 2007; Table 4). In cool-season grasses (rye [*Secale cereale*]-annual ryegrass [*Lolium multiflorum*]), daily concentrate supplementation of EW calves at 1.0%, 1.5%, and 2.0% of BW linearly increased calf ADG (0.74 to 0.89 kg/d; Table 4) while decreasing forage intake (18 to 11 g/kg BW). However, the net return did not differ among the different supplementation amounts (Table 4; Vendramini et al., 2006). Hence, optimal economic return occurred with daily concentrate supplementation at 1.0% and 1.5% of BW for EW calves grazing annual cool-season and perennial warm-season grasses, respectively.

Metabolic imprinting

Metabolic imprinting is the concept that nutrition during the early stages of a calf postnatal life may permanently change their development and long-term performance (Lucas, 1998). Cattle subspecies may also determine if metabolic imprinting will have positive or negative impacts on their performance. One example is the opposite responses in puberty attainment in Brangus vs. Nelore heifers following preweaning injections of bovine somatotropin (**bST**; Moriel et al., 2018; Piccolo et al., 2018). In both studies, preweaning injections of bST were implemented to boost the plasma concentrations of insulin-like growth factor I (IGF-I) during a critical period of reproductive axis development of beef heifers (3 to 6 mo of age), given that circulating IGF-I has been positively associated with puberty attainment (Moriel et al., 2014). However, preweaning injections of bST hastened the puberty attainment in Brangus heifers at the start of the breeding season (40% vs. 20% for bST and saline heifers, respectively; Piccolo et al., 2018) but decreased puberty attainment in Nelore heifers compared with preweaning injections of saline solution (25% vs. 40% for bST and saline heifers, respectively; Moriel et al., 2018). The discrepancy likely occurred due to an overstimulation of the somatotropic axis following bST injections in Nelore heifers, given that these young females had greater baseline plasma IGF-I concentrations compared with Brangus heifers (190 vs. 99 ng/mL, respectively). Accordingly, others have also noted greater basal concentrations of IGF-I in *B. indicus* females compared with counterparts with *B. taurus*-influence under similar nutritional and environmental conditions (Alvarez et al., 2000).

Creep feeding

Creep feeding is a supplementation strategy that can be used to overcome limited HP, increase energy and protein supply to nursing calves, provide adaptation to concentrate before weaning, and increase weaning weight in temperate, subtropical, and tropical areas (Faulkner et al. 1994; Carvalho et al., 2019). Creep-feeding supplements can be provided either ad libitum or limit-fed (Vendramini and Moriel, 2018). Ad libitum creep feeding increases calf preweaning growth, although concentrate intake to added gain ratio is often inefficient. As an example, *B. indicus*-influenced calves receiving creep feeding at 1% of BW had an added ADG of 0.12 kg/d compared with non-creep-fed calves, with a concentrate intake of 9 kg for every 1 kg of added BW gain (Vendramini et al., 2012). In contrast, limit creep-feed supplementation can be used as a strategy to alleviate the reduction in ruminal NDF digestibility and feed efficiency often associated with unlimited creep-feed supplementation (Cremin et al., 1991; Faulkner et al., 1994). Hand-feeding 0.23 kg/d of compressed range cubes (78% TDN and 37% CP; DM basis) for 100 d before weaning increased ADG of nursing *B. indicus*-influenced calves grazing bahiagrass pastures compared with non-creep-fed calves (0.94 vs. 0.86 kg/d, respectively), which corresponds to a concentrate intake of 2.9 kg for every 1 kg of added BW gain (Moriel and Arthington, 2013). Subsequent studies reported an added BW gain of 0.17 kg/d (Moriel et al., 2017) and 0.29 kg/d (Aguiar et al., 2015) for *B. indicus*-influenced calves grazing limpograss pastures and creep-fed 0.40 kg/d of soybean meal for approximately 83 to 90 d before weaning (2.4 and 1.4 kg of concentrate per kg of added BW gain, respectively). Lardy and Maddock (2007) summarized similar research outcomes in *B. taurus* cattle reared in temperate

Table 4. Growth response and economic analyses of early-weaned *Bos indicus*-influenced calves grazing rye-ryegrass pastures (Vendramini et al., 2006) or Tifton 85 bermudagrass pastures (Vendramini et al., 2007) and supplemented with increasing levels of concentrate

	Concentrate supplementation, % of BW					
Response	0	1.0	1.5	2.0	Response	SE
Vendramini et al. (2006)						
Calf daily gain, kg/d	—	0.74	0.81	0.89	Linear, $P < 0.01$	0.03
Stocking rate[1], AU/ha	—	5.5	5.9	6.5	Linear, $P < 0.01$	0.10
Concentrate cost, $/ha	—	600	970	1430	Linear, $P < 0.01$	25
Income, $/ha	—	2100	2370	2900	Linear, $P < 0.01$	91
Gross return, $/ha	—	1500	1400	1470	$P \geq 0.58$	92
Vendramini et al. (2007)						
Calf daily gain, kg/d	0.42	0.52	0.65	0.65	Linear, $P = 0.04$	0.02
Stocking rate[1], AU/ha	7.4	11.1	11.2	13.7	Linear, $P < 0.01$	0.40
Concentrate cost, $/ha	0	1100	1670	2710	Linear, $P < 0.01$	74
Income, $/ha	1540	2380	3200	3400	Linear, $P < 0.01$	190
Gross return, $/ha	1540	1280	1530	700	Quadratic, $P = 0.04$	284

[1] AU = animal unit (500 kg liveweight$^{0.75}$).

regions and concluded that concentrate intake to added gain ratio is mostly efficient when high-protein, limited-fed creep feeding is provided to nursing calves. Nonetheless, creep-feeding efficiency is often less in *B. taurus* compared with *B. indicus*-influenced breeds due to increased milk yield of *B. taurus* females, and subsequently less need for supplemental nutrients of their offspring (Lardy and Maddock, 2007).

Considerations in carcass composition

Bos indicus-influenced cattle are better suited for the production in tropical and subtropical regions, but often produce carcasses with less marbling scores than *B. taurus* cattle. To understand this latter relationship, research compared the de novo lipogenic capacity, adiposity, and fatty acid composition in *B. indicus*-influenced and *B. taurus* heifers and steers (Wheeler et al., 1990; Miller et al., 1991; St. John et al., 1991; Huerta-Leidenz et al., 1996; Campbell et al., 2016). Across all studies, the overall hypothesis was that intramuscular and subcutaneous adipocytes embedded in longissimus muscle (i.e., marbling adipocytes) were smaller in *B. indicus*-influenced cattle compared with *B. taurus* cattle. Moreover, it was also speculated that metabolic capacity for de novo fatty acid synthesis was less in the intramuscular adipose tissue from *B. indicus*-influenced cattle. Across all these experiments, days on feed were constant, and *B. taurus* and *B. indicus*-influenced cattle were at least three-fourths of each breed type. Adjusted fat thickness (**AFT**) was less in *B. indicus*-influenced than in *B. taurus* cattle except for Campbell et al. (2016), and the marbling score was also less for *B. indicus*-influenced cattle in all studies except for St. John et al. (1991; Table 5).

Adipocyte volume and metabolism

Intramuscular adipocytes were smaller than subcutaneous adipocytes (Schiavetta et al., 1990; Miller et al., 1991; Campbell et al., 2016; Smith et al., 2018) and the rate of de novo fatty acid synthesis was less in intramuscular adipose tissue across subspecies (Smith and Crouse, 1984; Miller et al., 1991; Campbell et al., 2016; Smith et al., 2018). In Miller et al. (1991), intramuscular and subcutaneous adipocyte volumes were less in Santa Gertrudis (*B. indicus*) steers compared with Angus (*B. taurus*) steers (Figure 6), consistent with the lower marbling score and AFT for the Santa Gertrudis (Table 5). For Campbell et al. (2016), intramuscular adipocyte volume and marbling score were less in *B. indicus*-influenced than in Angus cattle (Table 5 and Figure 7). Subcutaneous adipocyte volume and AFT were not different between *B. indicus*-influenced and Angus cattle. Marbling score increases by the combined processes of intramuscular adipocyte proliferation and hypertrophy (Moody and Cassens, 1968; Brooks et al. 2011). It is possible that the muscle tissue of *B. indicus* lacks the necessary stem cells for proliferation and differentiation into intramuscular adipocytes, but our results indicate that lesser marbling score in *B. indicus*-influenced cattle (relative to *B. taurus* cattle) is the result of a lesser capacity for their adipose tissues to synthesize lipids de novo.

Table 5. Subcutaneous fat thickness and marbling score for *Bos taurus* and *B. indicus*-influenced steers and heifers measured at the 12th thoracic rib

	Fat thickness, cm		Marbling score[1]	
Reference	*B. taurus*	*B. indicus*	*B. taurus*	*B. indicus*
Wheeler et al. (1990)	1.04[a]	0.73[b]	78[a]	180[b]
Miller et al. (1991)	1.55[a]	0.91[b]	112[a]	218[b]
St. John et al. (1991)	1.19[a]	0.86[b]	195[a]	387[a]
Huerta-Leidenz et al. (1996)	1.08[a]	0.70[b]	174[a]	271[b]
Campbell et al., (2016)	1.37[a]	1.19[a]	256[a]	368[b]

[1] 000 = Practically devoid; 100 = Slight; 200 = Modest.

[a,b] Means with the same trait with different superscripts differ ($P \leq 0.05$).

Enzymes associated with de novo fatty acid biosynthesis, as well as glucose and acetate incorporation into fatty acids, were also measured across these experiments (Smith and Crouse, 1984; Miller et al., 1991; Smith et al., 2018). For example, NADP-malate dehydrogenase (**NADP-MDH**) activity was less in intramuscular and subcutaneous adipose tissues from *B. indicus*-influenced steers than in *B. taurus* steers (Miller et al., 1991; Figure 6). Greater NADP-MDH activity usually indicates greater capacity to incorporate glucose into fatty acids (Prior et al., 1981; Smith and Prior, 1981; Smith and Crouse, 1984; Smith et al., 2018), but the rate of fatty acid synthesis from glucose was not different in intramuscular and subcutaneous from *B. indicus*-influenced and *B. taurus* steers (Figure 6). Instead, the rate of fatty acid synthesis from acetate was less in intramuscular adipose tissue from *B. indicus*-influenced than in intramuscular adipose tissue from *B. taurus* steers. St. John et al. (1991) reported that adipocyte volume and NADP-MDH activity were not different in subcutaneous adipose tissue from Angus and Braford (*B. indicus*-influenced) heifers, even though AFT was less in Braford heifers than in Angus heifers (Table 5). Thus, adipocyte metabolic capacity measured in vitro was not always consistent with carcass measures of adiposity in this series of experiments.

A subsequent study (Huerta-Leidenz et al., 1996) demonstrated that the proportion of oleic acid (18:1n-9) was greater in subcutaneous adipose tissue from Hereford (*B. taurus*) steers than in subcutaneous adipose tissue in Brahman (*B. indicus*) steers, suggesting that fatty acid $\Delta 9$ desaturase enzyme activity (stearoyl-CoA desaturase [**SCD**]) was greater in subcutaneous adipose tissue from *B. indicus* cattle. However, no difference in SCD activity of subcutaneous adipose tissue from *B. taurus* and *B. indicus*-influenced cattle was noted by St. John et al. (1991). This was supported more recently in a comprehensive study comparing three-fourths Brahman progeny to three-fourths Angus progeny (Campbell et al., 2016), in which progeny were raised to a constant age and constant AFT. There was no difference between the proportions of stearic acid (18:0) and oleic acid in subcutaneous adipose tissue between progenies, nor was there a difference in subcutaneous or intramuscular adipose tissue SCD activity. The results of Campbell et al. (2016) would seem to rule out a genetic basis between *B. indicus*-influenced and *B. taurus* cattle to desaturate stearic acid (18:0) to oleic acid.

Collectively, this series of experiments indicate that intramuscular and subcutaneous adipocytes are typically smaller in *B. indicus*-influenced cattle compared with *B. taurus* counterparts. No strong relationship between the capacity to synthesize fatty acids de novo and marbling score or adipocyte volume was noted. Therefore, the reduced marbling score typically observed in *B. indicus*-influenced cattle should be mainly attributed to their smaller intramuscular adipocyte volume compared with *B. taurus* breeds.

Summary and conclusions

Beef production needs to increase in 120% by 2050 to feed a growing world population, and 70% of this production increase is expected from beef industries located in subtropical and tropical

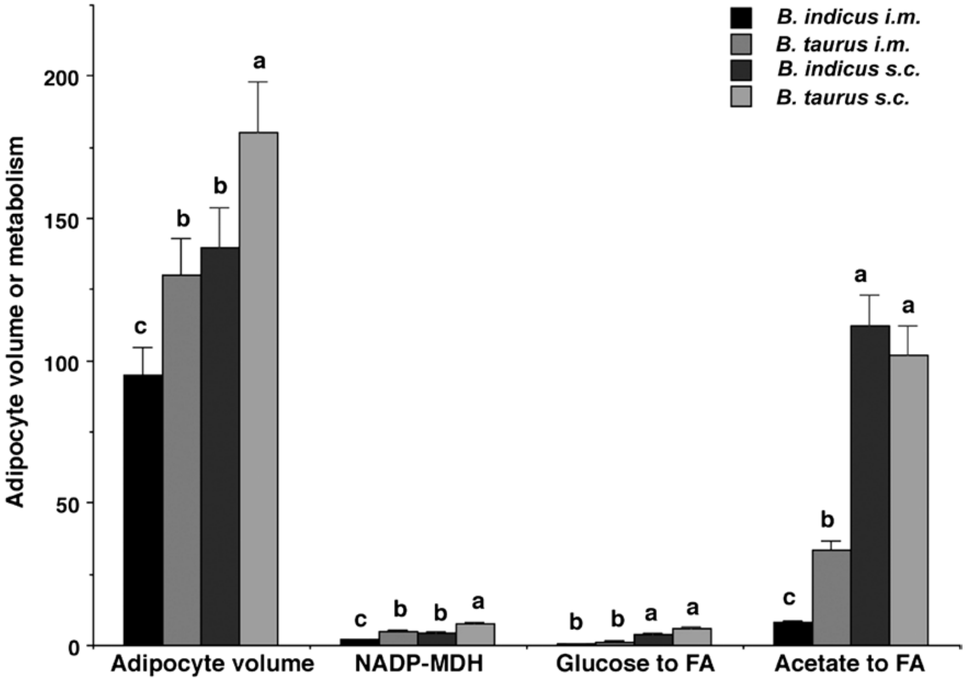

Figure 6. Adipocyte volume (pL) and adipocyte metabolism (nmol•2 h^{-1}•10^{5} cells^{-1}) for intramuscular (**i.m.**) and subcutaneous (**s.c.**) adipose tissues from *B. indicus*-influenced and *B. taurus* steers and heifers. Metabolic variables include NADP-MDH, glucose carbon incorporated fatty acids (**FA**), and acetate carbon incorporated into FA. Means within a trait with different superscripts (a,b,c) differ ($P \leq 0.05$). Data derived from Miller et al. (1991).

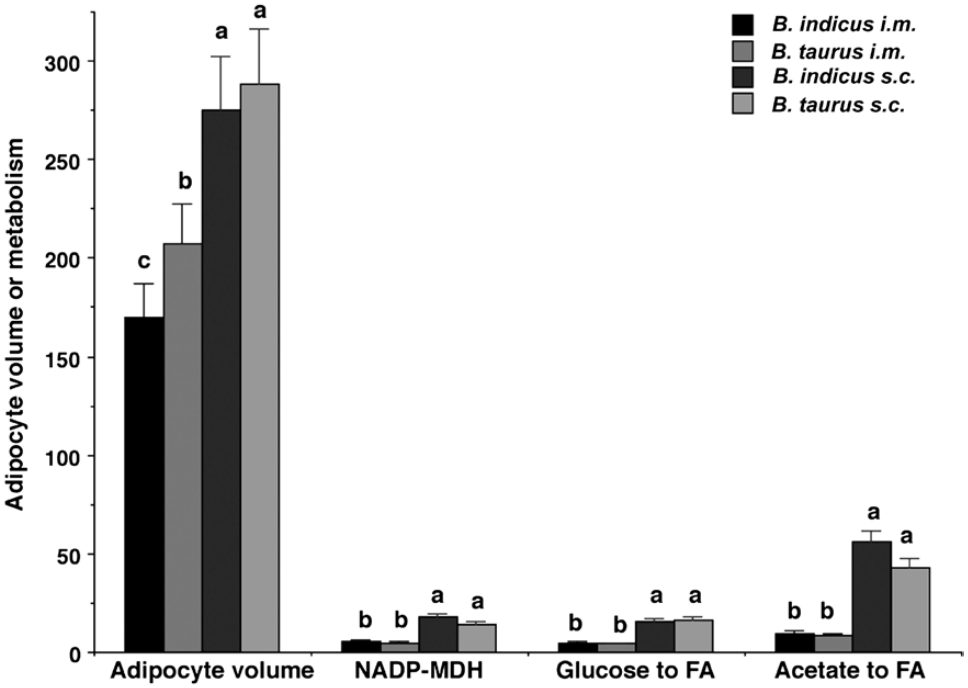

Figure 7. Adipocyte volume (pL) and adipocyte metabolism (nmol•2 h^{-1}•10^{5} cells^{-1}) for intramuscular (**i.m.**) and subcutaneous (**s.c.**) adipose tissues from *B. indicus*-influenced and *B. taurus* steers and heifers. Metabolic variables include NADP-MDH, glucose carbon incorporated fatty acids (**FA**), and acetate carbon incorporated into FA. Means within a trait with different superscripts (a,b,c) differ ($P \leq 0.05$). Data derived from Campbell et al. (2016).

regions of the planet. *Bos indicus*-influenced cattle predominate in these regions and are typically managed using practices developed for *B. taurus* breeds in temperate zones, despite being different subspecies reared in different environmental conditions. *Bos indicus* cattle display distinct social responses compared with *B. taurus* counterparts, which must be taken into account by management planning as these traits directly impact cattle performance and welfare. Nutritional planning in tropical and subtropical conditions must also include management to optimize utilization of warm-season forages, whereas nutritional requirements of cattle raised within these conditions still need to be further established. As an example, *B. indicus*-influenced cattle appear to have an intrinsic metabolic compromise to cope with environmental constraints, and altered energy requirements due to body composition and heat tolerance. Accordingly, nutritional interventions to enhance beef production need to be specifically tailored and validated in *B. indicus*-influenced cattle. *Bos indicus*-influenced cattle also produce carcasses with less marbling than *B. taurus* cattle. This outcome is mostly related to reduced intramuscular adipocyte volume in *B. indicus* breeds, which may be an inherent mechanism to facilitate heat dissipation and grant the thermotolerance required for adaptation to tropical and subtropical climates. Nonetheless, there is still a plethora of research-based information needed to fully comprehend the social and welfare aspects, nutrient demand and use, and carcass development of *B. indicus*-influenced cattle. Efforts to understand biological functions specific to this cattle subspecies are critical to optimizing beef production in tropical or subtropical environments and meet the increasing global demand for beef.

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Conflict of interest statement

No conflict of interest to disclose.

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