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REVIEW ARTICLE

An updated review on cattle thermoregulation: physiological responses, biophysical mechanisms, and heat stress alleviation pathways

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Abstract
Heat stress is one of the main obstacles to achieving efficient cattle production systems, and it may have numerous adverse effects on cattle. As the planet undergoes climatic changes, which is predicted to raise the earth's average temperature by 1.5 °C between 2030 and 2052, its impact may trigger several stressful factors for livestock. Among these, an increase in core body temperature would trigger physiological imbalance, consequently affecting reproduction, animal health, and dry matter intake adversely. Core body temperature increase is commonly observed and poses challenges to livestock farmers. In cattle farming, thermal stress severely affects milk production and weight gain, and can compromise food security in the coming years. This review presents an updated approach to the physiological and thermoregulatory responses of cattle under various environmental conditions. Strategies for mitigating the harmful effects of heat stress on livestock are suggested as viable alternatives for the betterment of production systems.

Keywords *Bos indicus* · *Bos taurus* · Climate changes · Cutaneous evaporation · Heat stress mitigation · Sensible heat loss

Introduction

The growing concern with global food security (Henry et al. 2018) led researchers, technicians, and farmers to seek increasingly adapted and efficient animals to develop commercial herds. Understanding this current concern is necessary when analyzing the world panorama of animal production and directing research to increase the productivity and efficiency of agricultural systems. According to the Brazilian Association of Meat Exporting Industries (ABIEC 2019), Brazilian meat production has gained prominence in recent years. This is due to the large volumes of meat exported, mainly commercial cattle—breeds of the species *Bos indicus*—which have adapted to the tropical climatic conditions.

However, climatic variations leading to an increase in the planet's surface temperature by 1.5 °C between 2030 and 2052, mainly due to anthropogenic activities (IPCC 2018), have been predicted. This climate change is worrisome for livestock activity, as they may lead to several stressful factors for the animals. These deleterious effects include increased core body temperature, triggering a physiological imbalance, with consequent adverse effects on reproduction, animal health, and dry matter intake, making it challenging for livestock farmers to improve animal production (Batista et al. 2015; Das et al. 2016; Sammad et al. 2020). Air temperature, relative humidity, wind speed, and solar radiation are environmental components that contribute to thermal stress in animals (Costa et al. 2018b; Berman 2019). When they are not protected from these meteorological elements, cattle tend to decrease their production, which may jeopardize food security in the coming years.

The precariousness of the updated information regarding how cattle respond biophysically and physiologically to hot environments, besides the viable strategies to deal with heat-adverse situations, has been verified. In this review, an updated approach to the physiological and thermoregulatory responses of cattle under various environmental conditions has

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been provided. Strategies for mitigating the harmful effects of climate change on livestock have also been suggested.

Thermal stress in cattle

Heat stress (HS) is considered one of the main barriers for an efficient production system, and it may have numerous adverse effects in cattle. In general, HS increases body temperature and activates the hypothalamus–pituitary axis, causing increased water consumption and consequently a decrease in dry matter intake, resulting in weight loss and delay in body development. HS can also lead to death in extreme cases (Kamal et al. 2018).

In cattle production, severe thermal stress can decrease milk production and delay weight gain (Baumgard and Rhoad Jr 2013). The effects of climate variables such as air temperature, wind speed, relative humidity, and solar radiation can negatively affect animals, especially cattle exposed to direct solar radiation (Santos et al. 2019; Abdelnour et al. 2019).

Cattle can maintain a relatively constant core body temperature within narrow limits. In situations of thermal discomfort (cold or heat), these animals activate thermoregulatory mechanisms to regulate the internal temperature that remain within acceptable physiological limits (Godyń et al. 2019).

The homeothermy chart, which is subdivided into three thermal zones: thermoneutral zone, homeothermy, and survival zone, is illustrated in Fig. 1. Limited between lower critical temperature (LCT) and upper critical temperature (UCT) in the thermoneutral zone, the animals are in the thermal comfort range, and the metabolic rate is minimal (Godyń et al. 2019). Under this condition, the animal does not activate physiological mechanisms to dissipate heat to the environment or generate endogenous heat, hence maintaining a body temperature that is balanced with the environment and allocating all the available energy to maximize performance (production, reproduction, among others). In this situation, the sensible mechanisms of heat exchange are sufficient to maintain thermal equilibrium.

In the homeothermy zone, the ambient temperature increases and exceeds the upper critical temperature limit; this challenges the animals from activating evaporative thermolysis mechanisms (Kamal et al. 2016; Sejian et al. 2018). With the environmental temperature variation reaching the limit of the UCT, cattle modify their behavior; for example, they begin to seek shade, increase water intake, and decrease feed intake, in addition to lying next to colder surfaces to try and balance the thermal change (Ratnakaran et al. 2017; Madhusoodan et al. 2019). When the lower critical temperature is reached, the animals' thermoregulatory system is activated to retain body heat and/or to produce endogenous heat (thermogenesis). This is achieved by increasing feed intake to generate metabolic heat through the breakdown of nutrients in the digestive system and modifying their behavior for heat retention, such as forming groups, avoiding lying on cold surfaces, and direct exposure to solar radiation if they have access.

If the environmental temperature increases or decreases, the animals will show hyperthermia and hypothermia, respectively (Fig. 1). In these cases, body protein denaturation occurs with consequent damage to physiological functions (Bettaieb and Averill-Bates 2015). If the environmental conditions are not altered to provide thermal comfort, the animals may die. In this scenario, understanding the animals' comfort zone is crucial for decision-making in order to provide

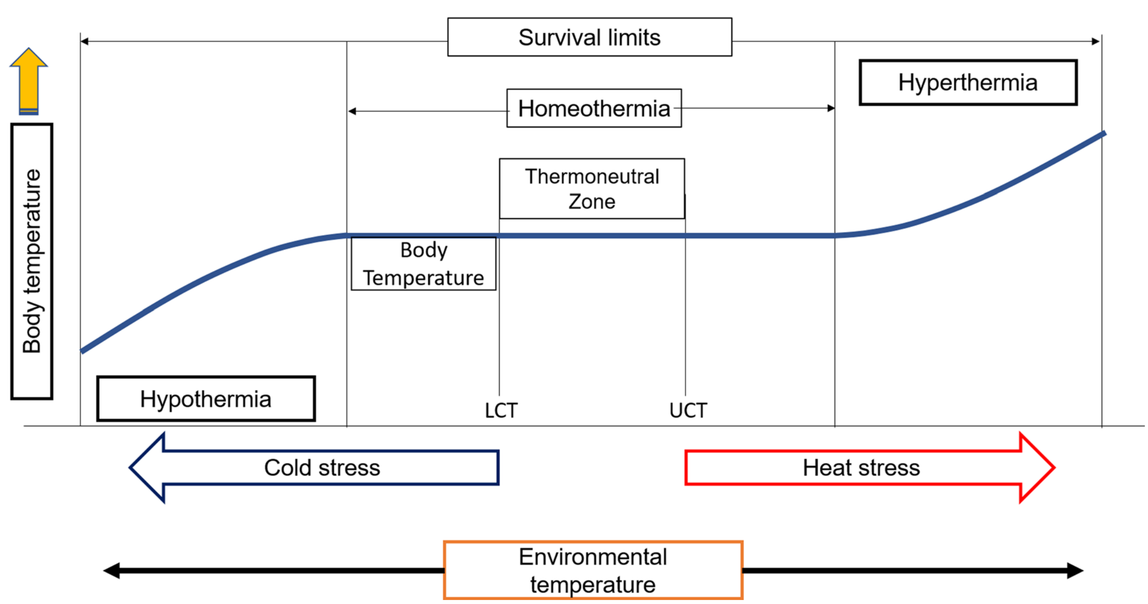

Fig. 1 Body temperature variation with an increase or decrease in environmental temperature. Adapted from Ehrlemark and Sallvik (1996). LCT is the lower critical temperature, and UCT is the upper critical temperature

environments that mitigate the thermal stress impact and where the animals express the maximum of their genetic potential productive.

Physiological responses

To survive in extreme environmental conditions, animals seek to modify their behavior and physiology to withstand stressful conditions (Fig. 2). Exposure of animals to high temperatures and solar radiation increases the body temperature, and this excess body heat needs to be dissipated (Table 1). This causes more intense physiological activity, as evidenced by the increase in respiratory rate, rectal temperature, and body surface temperature (Sharma et al. 2013; Rashamol et al. 2018; Saizi et al. 2019; Habeeb et al. 2020).

Rectal temperature

Body temperature is determined by the balance between heat loss and gain, referenced by the rectal temperature, which can vary from 38.65 to 39.05 °C in different Zebu breeds (Cardoso et al. 2015). When exposed to HS, the animals try to dissipate as much heat as possible to balance their body temperature. An increase in their rectal temperature (RT, °C) may occur under thermally stressful environmental conditions (Rashamol et al. 2018). In an environment where the air temperature amplitude exceeds 10 °C, ranging from 20 to 35 °C, the RT of Nellore cattle protected from solar radiation remained practically constant (39.0 to 39.4 °C). The efficiency of thermoregulatory mechanisms to maintain body temperature within narrow limits has been verified (Costa et al. 2018b). In grazing conditions in a tropical environment, Nellore cattle show a small RT change ranging from 38.9 to 39.2 °C (Menegassi et al. 2016).

In tropical regions, high loads of solar radiation can cause negative effects on the physiology and thermoregulation of animals (Table 1), becoming an aggravating factor for thermal stress and consequently leading to a decrease in productive performance (Nardone et al. 2010; Gaughan et al. 2010a, b). When exposed to solar radiation, RT of Nellore cattle showed a small amplitude of 38.4 to 38.6 °C. However, variations smaller than 0.5 °C in the RT of Zebu cattle under different environmental conditions indicate that these animals' thermoregulatory mechanisms are fairly efficient in maintaining their RT constant regardless of air temperature variation and direct solar radiation (Santos et al. 2019).

Respiratory rate

The respiratory rate (RR, breaths/min) in cattle is easily detected by observing flank movements. This physiological indicator dissipates excess heat in the environment (Sailo et al. 2017). In thermal stress situations, animals tend to raise RR to increase the respiratory evaporation rate and thus lose heat to the environment. In *Bos indicus*, the average RR may vary from 33.75% to 41 breaths/min according to race, air temperature, and time of day (Cardoso et al. 2015). In animals from crossbreeding between *Bos Taurus* and *Bos indicu*s, RR may also vary according to seasons, ranging from 40.8 breaths/min, 38.7 breaths/min, and 33.2 breaths/min in winter, spring, and summer, respectively (Romanello et al. 2018). Contrastingly, RR in *Bos taurus* (Karan Fries breed) was higher during summer (47.30 breaths/min) when compared

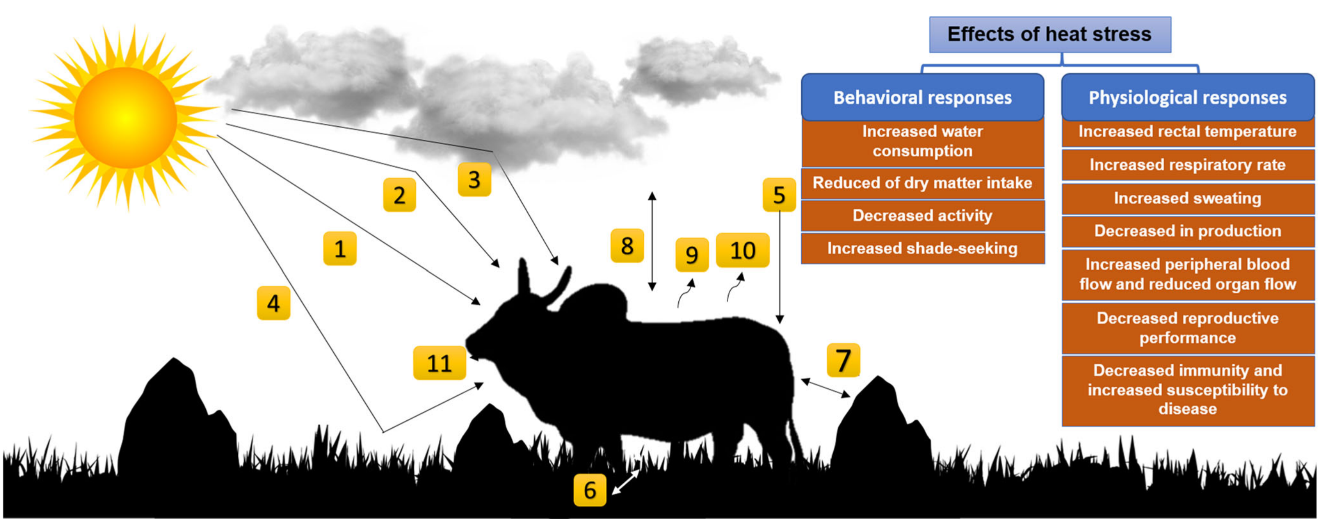

Fig. 2 Description of the heat stress effects on the behavioral and physiological responses of cattle. 1 Direct short-wave solar radiation; 2 diffuse radiation; 3 short-wave radiation reflected by clouds; 4 short-wave radiation reflected from the soil surface; 5 celestial short-wave radiation; 6 conduction heat exchanges; 7 long-wave radiation emitted by the surrounding area; 8 heat exchange for long-wave radiation; 9 heat loss by cutaneous evaporation; 10 convection heat exchange; 11 heat loss by pulmonary evaporation

Table 1 Main factors that influence the physiological and biophysical responses of cattle

Breed	Gender	Factor	Geographic location	Main outcomes	Authors
Nellore	Male	Temperature	Brazil	In environments with a temperature above 30 °C, most of the heat produced by metabolism is dissipated via cutaneous evaporation.	Costa et al. (2018a)
Nellore	Male	Circadian pattern	Brazil	There is less energy expenditure due to heat loss during the night, where animals use sensible mechanisms more efficiently. During the day, evaporative mechanisms become more important for thermoregulation.	Costa et al. (2018b)
Guzerat	Male and female	Thermal balance	Brazil	A lower respiratory rate indicates better handling and can be used as a selection criterion. The air temperature directly influences the haircoat and skin temperatures and expired air temperature, whereas the rectal temperature depends on the time of day. Sensible heat flow decreases with increasing temperatures; however, the heat loss in respiratory via practically did not vary with increasing temperature.	Camerro et al. (2016)
Holstein	Female	Evaporative and non-evaporative heat loss	Brazil	In environments with high temperatures, cutaneous evaporation corresponds to 85% of Holstein cows' total heat loss, whereas sensible heat exchange becomes inefficient when animals are thermally challenged.	Maia et al. (2005a)
Holstein	Female	Respiratory heat loss prediction	Brazil	In tropical environments with an air temperature above 20 °C, evaporation heat loss becomes increasingly high. Convection heat exchange is less critical for heat loss, whereas respiratory evaporation is an effective means of dissipating heat.	Maia et al. (2005b)
Holstein	Female	Exposure to the sun; haircoat pigmentation	Brazil	Holstein cows with a black haircoat have a higher sweating rate, cutaneous thermolysis, and surface temperature than cows with a white haircoat.	Silva and Maia (2011)
Holstein, Simental, Canchin, Brangus e Nellore.	Female and male	Short-wave solar radiation on hair and skin properties	Brazil	The white coat has a greater reflectance capacity than the black hair coat. Non-pigmented skins have lower reflectance values. Pigmented skin and white hair coat suggest greater protection against ultraviolet radiation, with reduced body surface heating by long-wave radiation.	Silva et al. (2003)
Girolando (½Holstein ½ Gir vs. ¾ Holstein ¼ Gir)	Female	Physiological, productive, and reproductive parameters	Brazil	Girolando cows (½ Holstein ½ Gir) show normal respiratory rate and rectal temperature, better reproductive parameters, and greater thermoregulatory capacity than Girolando cows (¾ Holstein ¼ Gir).	Costa et al. (2015)
Nellore	Male	Exposure to solar radiation	Brazil	During times of the day with high direct solar radiation, Nellore bulls trigger thermoregulatory mechanisms involving the respiratory system to maintain body temperature within narrow limits.	Santos (2020)
Angus e Simental	Male	Heat adaptation	Brazil	The season affects the morphological and physiological aspects of Angus and Simental cattle raised in Brazil. The Simental breed is more heat-tolerant than the Angus breed.	Baena et al. (2019)
Canchin	Male	Thermoregulatory and reproductive responses	Brazil	Even under a progressive thermal challenge, the scrotal thermoregulatory capacity of Canchin bulls was not affected, which was maintained at 5.2 °C below the internal body temperature. The thermoregulatory ability of these animals indicates a viable alternative for breeding in a tropical environment.	Romanello et al. (2018)
Sahiwal e Karan Fries	Female	Effect of the seasons on thermoregulation	India	Sahiwal cows are less sensitive to temperature increases during the summer, presenting a high thermoregulatory capacity due to lower metabolic rate and high sweating capacity than the Karan Fries breed.	Sailo et al. (2017)

with that during other seasons (Sailo et al. 2017). In a study by Santos et al. (2019) evaluating the thermophysiological characteristics of Nellore bulls exposed to solar radiation, they found that throughout the day, the respiratory frequency of these animals ranged from 27 to 36 breaths/min. However, a variation of 7 breaths/min becomes an insignificant value to be considered an indication of heat stress in the animals (Romanello et al. 2018), even presenting differences according to Zebu breeds and crossings, as well as season, time of day, and exposure to solar radiation. The thermoregulation of *Bos taurus* cattle can be affected when situated in the Brazilian tropical climate; the RR exceeds 80 breaths/min especially at the day's hottest times (Baena et al. 2019). Despite the productivity attributed to *Bos taurus* cattle, its low tolerance to warm climate regions is an important decision criterion for this species breeding in this climate type because we can choose more adapted animals (Zebu) to environments with high temperatures and solar radiation.

Body surface temperature

The body surface temperature (BST, °C) of cattle can be measured using an infrared sensor (Santos et al. 2019) and infrared thermography, a non-invasive method capable of measuring the infrared radiation emitted from the surface of an animal's body (Church et al. 2016; Sejian et al. 2018). The surface temperature of an animal can be measured at various regions, such as the dorsum, flanks (Romanello et al. 2018), ocular region, snout, and cheeks (Montanholi et al. 2009; Colyn 2013)

Surface temperature is an essential response to thermal stress, which is directly influenced by the environment in which the animal is subjected, such as air temperature and radiation (Lima et al. 2020). When these environmental variables are high, BST tends to increase, leading to peripheral vasodilation. This is verified by increasing blood flow in the capillaries, which facilitates heat dissipation to the environment (Katiyatiya et al. 2017; Madhusoodan et al. 2019).

The characteristics of the animal's coat also influence BST, where, in tropical environments, the white haircoat, dark epidermis, and short and dense hair favor the thermal equilibrium of the production animals (Maia et al. 2005a, b; Romanello et al. 2018). Coat color is a crucial feature of radiation (McManus et al. 2011). When direct solar radiation reaches the surface of the animal's skin, some is reflected, and the remaining is absorbed. In animals with predominantly white haircoats, approximately 60–67% of animal solar radiation is reflected in the environment (Silva et al. 2003).

The increase in air temperature and the high incidence of solar radiation can elevate the BST (Carvalho et al. 2019). BST variation can be observed in animals of different breeds under direct solar radiation exposure and high air temperature. Studies carried out by Lima et al. (2020) with bulls of the Nellore and Caracu breed during the summer and exposed to the sun, it was found that Nellore animals had a BST of 41.5 °C, whereas the Caracu breed had 44.2 °C. This difference may have been explained by the color of the animals' coats, as white surfaces reflect more radiation than they absorb relative to darker-colored surfaces. In shaded environments, there is no significant difference in BST for animals of the same breed (Camerro et al. 2016) or between different breeds (Lima et al. 2020), verifying that BST is mainly influenced by environmental factors such as air temperature and solar radiation.

Biophysical mechanisms of thermal exchange

Animals can lose heat through sensible and latent heat exchange. For thermal exchange by sensible mechanisms to occur, there must be a temperature difference between the animal's body and the environment; that is, the heat loss occurs when the animal's body temperature is higher than the environmental temperature (Collier and Gebremedhin 2015a, b). It is understood that sensible heat loss occurs through conduction, convection, and radiation. When the environmental temperature is equal to or higher than that of the animal's body, the sensible heat exchange becomes insignificant and can be a heat gain pathway, respectively (Collier and Gebremedhin 2015a, b). Environmental conditions, such as air temperature and relative humidity, are important variables that cause changes in cattle thermoregulation. These variables are fundamental for estimating the heat exchange between the animal and the environment, although there are other important factors, such as wind speed and solar radiation (Herbut et al. 2018; Godyń et al. 2019). Variations in wind speed directly affect cooling through convection, which can positively or negatively impact solar radiation exposure (Herbut et al. 2013; Godyń et al. 2019).

Exposure to direct solar radiation challenges animals' thermoregulation. When cattle encounter environmental temperatures above their body temperature, they activate latent heat loss mechanisms, known as skin and respiratory evaporation. These latent mechanisms do not depend on the temperature gradient between the environment and the animal's body surface. However, air humidity plays a key role in evaporation efficiency. When the relative humidity of air is high, the amount of water in the form of steam in the air is also high, affecting the heat loss efficiency by evaporation (Baena et al. 2019).

Sensible mechanisms

There are three types of sensible heat transfer mechanisms between animals and their environment: long-wave radiation, convection, and conduction. In these mechanisms, the temperature gradient between the animal's body and the environment determines the direction of heat transfer (loss or gain). When the animal's temperature is higher than that of the environment, the animal loses heat to its environment. However, when the environmental temperature is higher than that of the animal, the above mechanisms become heat gain pathways for the animal (Collier and Gebremedhin 2015a, b). If this occurs in excess, it may cause physiological damage and loss of production.

Long-wave radiation

Heat exchange with long-wave radiation occurs via thermal energy transfer through electromagnetic waves. According to Berman (2014), the animal's position, standing or lying, influences body heat dissipation through long-wave radiation. When the animal is lying down, heat loss due to radiation is reduced. The same author also reported that, in shaded environments where cattle are present in close proximity, there is heat loss by long-wave radiation due to less exposure of the animals' body surface, and the proximity between two bodies causes a heat gain. There is an increase in the amount of heat dissipated by other mechanisms in this situation.

Nellore cattle in the tropical region are protected from the sun and have a heat loss from radiation between 36 and 52 $W.m^{-2}$ throughout the day. Therefore, they suffer a decrease in the hottest times of day (12:00 to 14:00), where the average radiant temperature rises above the surface temperature of the animal, which is a route of heat gain (Costa et al. 2018a). In Holstein cows located in warm, shaded environments, 60 $W.m^{-2}$ of heat loss by radiation was verified during the lactation period (Berman 2014). Protection from direct solar radiation favors heat exchange via long-wave radiation in Nellore cattle. Under these conditions, the BST was observed to be higher than the mean radiant temperature, corresponding to a heat loss of 40 $W.m^{-2}$ between 10:00 and 14:00 h (Costa et al. 2018b). However, when Nellore cattle are not protected from direct solar radiation in a semi-arid environment, the exchange of heat for long-wave radiation becomes a gain route, reaching an average gain of 250 $W.m^{-2}$ during the hottest times of the day (Santos 2020).

Convection

Heat transfer by convection depends on the thermal gradient between the body surface of the animals and the environment. Wind velocity directly influences heat loss due to convection (Schutz et al. 2010; LokeshBabu et al. 2018), breaking the resistance of the boundary layer of the bovine body surface (Berman 2019) and changing the body surface temperature.

Convection can be natural, forced, or combined. Natural convection depends on air movement over the surface of an animal's body caused by a change in air density from the temperature difference between the boundary layer and the atmosphere (Collier and Gebremedhin 2015a, b). Forced convection occurs due to the difference in external pressure on the animal's body, usually associated with mechanical systems (Collier and Gebremedhin 2015a, b). In many circumstances, natural convection is associated with forced convection. In such cases, to verify the type of convection occurring, a relationship between the dimensionless numbers of Grashoff (Gr) and Reynolds (Re) is considered: if $Gr/Re^2 \geq 3.0$, the convection is natural; if $Gr/Re^2 \leq 0.08$, the convection is forced; when Gr/Re^2 is between 0.08 and 3.0, the convection is combined (Silva 2008).

In experiments with Nellore cattle protected from the sun, Costa et al. (2018b) verified heat loss by convection at times of day when the air temperature was lower than 25 °C (00:00–08:00 and 16:00–23:00). The heat loss by convection showed values of 27 to 40 $W.m^{-2}$. This heat loss can also be explained by the temperature difference between air and the body surface, as the amplitude between them at times of day reached 10 °C. The heat exchange by convection in Nellore bulls to the sun may correspond to a loss of 70 $W.m^{-2}$ on average between 11:00 and 17:00, which is favored by the temperature gradient between BST and air temperature influenced by wind speed (Santos 2020).

Conduction

Heat exchange by conduction occurs by direct contact between two surfaces through the displacement of the kinetic energy of the molecules that are more energized to the ones that are less energized (Silva and Maia 2013). Heat loss by conduction can be significant when an overheated animal comes into contact with wet surfaces (Oliveira et al. 2014). However, it avoids lying on soil surfaces where the temperature is higher than its body temperature, avoiding heat gain by conduction (Oliveira et al. 2019). Conduction may be insignificant when the animals are standing, mainly due to a reduction in their contact with the colder surface (Collier and Gebremedhin 2015a, b).

Evaporative thermolysis mechanisms

The constant variation in the environmental temperature hinders sensible heat dissipation, activating latent heat loss mechanisms, and increasing respiratory and cutaneous evaporation. According to Maia et al. (2005a), in adult cattle, cutaneous evaporation is responsible for 85% of latent heat dissipation, while the rest occurs by respiratory evaporation. However, this way of losing heat may be difficult as the relative humidity and temperature of the air meet, if elevated, leading to thermal stress by failing to dissipate excess heat.

Cutaneous evaporation

In a tropical environment, sweating is the main route for cattle to lose the excess heat they gain from the environment; however, despite this, *Bos taurus* shows significant productive losses in high-temperature environments (García et al. 2020). Exposure of cattle to thermally stressful conditions triggers physiological reactions such as peripheral vasodilation, and stimulation of the sweat glands in an attempt to dissipate excess body heat (Godyń et al. 2019). The effectiveness of evaporative cooling on the surface of the skin can be influenced by the density, thickness, hair length, epidermal characteristics, and coat coloration (Gebremedhin et al. 2008; Madhusoodan et al. 2019). In tropical environments, short, thick, and settled haircoats help increase the maximum heat dissipation during heat stress conditions (Da Silva et al. 2003).

According to Silva and Maia (2011), cutaneous evaporation remains unchanged with an average of 48 W.m^{-2} until the body surface temperature reaches 31 °C. While studying the thermal balance of Nellore cattle, Costa et al. (2018b) found a cutaneous evaporation variation of 42.12 to 85.67 W.m^{-2} when the body surface temperature was between 32 and 36 °C. The same authors also reported that this variation in latent heat loss on the body surface is due to positive correlations with air temperature ($r = 0.92$), haircoat temperature ($r = 0.87$), and skin temperature ($r = 0.87$), which led to a total heat loss of 53%.

The Zebu cattle in the tropical zone under the shade had a surface temperature of 36 °C and reached maximum values for heat loss by cutaneous evaporation of only 64.75 W.m^{-2} (Costa et al. 2018a) and 85.67 W.m ^{2} (Costa et al. 2018b). However, the results found for cutaneous evaporation in Nellore cattle exposed to the sun were fascinating (Santos 2020). Even with the aggravating solar radiation during the day, the average cutaneous evaporation did not exceed 80 W.m^{-2} during warmer periods.

Cutaneous evaporation may vary depending on the region of the animal's body and hair color. Studying latent heat loss in dairy cows in a semi-arid equatorial environment, Silva et al. (2012) observed significant differences in cutaneous evaporation between the neck, flank, and hindquarters with values of 133.3, 116.2, and 98.6 W.m^{-2}, respectively. Haircoat color is also of significant importance for heat loss due to skin evaporation. Black-haired cattle in semi-arid environments have a surface temperature of 35.49 °C, and cutaneous evaporation of 186.32 W.m^{-2}; however, in cattle with white haircoat, the surface temperature and cutaneous evaporation are of 35.05 °C and 158.24 W.m^{-2}, respectively, where this surface temperature difference explains a greater absence of black haircoat (Santos et al. 2017). Silva et al. (2012) also observed a similar trend for black haircoat, where the skin surface temperature was 41.7 °C and cutaneous evaporation was 117.0 W.m$^{-2,}$ and for white haircoats, the values were 37.2 °C and 106.7 W.m^{-2}, respectively.

Respiratory evaporation

Respiratory evaporation is a latent mechanism of heat loss that depends directly on the respiration rate (Maia et al. 2005a) because it occurs through the airways (Spiers et al. 2018), in which the latent heat of water vaporization is used in an attempt to dissipate body thermal energy (Santos et al. 2017).

Panting is a physiological response of many animals to heat stress, which intensifies heat loss by evaporation due to increased respiratory rate and decreased tidal volume, resulting in an increase in respiratory tract ventilation (Renaudeau et al. 2012; Collier and Gebremedhin 2015a, b). In the semi-arid environment, dairy cows of the Holstein breed have an average respiratory rate of 78 breaths.min^{-1} due to high environmental temperatures (33.1 °C), attributing a higher stress condition to these animals that respond with an increase in respiratory evaporation of 44.0 W.m^{-2} leading to a total latent heat loss of 27.3% (Silva et al. 2012). In Zebu animals present in a tropical environment and protected from the sun, the respiratory rate and heat loss by respiratory evaporation did not exceed 27 breaths.min^{-1} and 15 W.m^{-2}, respectively (Costa et al. 2018a). The contribution of this thermolysis mechanism is insignificant for maintaining thermal equilibrium in this type of environment (Camerro et al. 2016; Costa et al. 2018a; Costa et al. 2018b).

In a semi-arid environment, respiratory evaporation in sun-exposed Nellore bulls during the day represented 40.55% of the total evaporative heat loss, ranging from 35 to 45 W.m^{-2}. The efficiency of this mechanism in maintaining thermal equilibrium has been verified since the respiratory rate did not exceed 36 breaths.min^{-1} and body temperature remained at 38.5 °C (Santos 2020).

Heat stress alleviation pathways

Climate change, especially the expected increase in temperature by the year 2065, has posed a challenge for animal protein production. There are many problems that this global temperature rise could cause. Nardone et al. (2010) explained that it may have several impacts on animal production: decrease in meat and milk productivity, reproduction impaired by higher temperature sensitivity and consequently lower fertility, and animal health being more susceptible to morbidity and mortality. The climate vulnerability we may face in the coming years can directly affect global food security; however, the search for solutions to these events has been researched and tested to adapt to the harmful effects of climate on animal production (Berman 2019). Thus, understanding how animals respond to thermal stress would favor the adequacy of environmental and genetic selection, as well as nutritional strategies (Table 2) to improve thermal comfort, animal welfare, and profitability of livestock activity. These strategies are addressed in the following sections.

Physical changes in the environment

Protecting animals from direct solar radiation can provide comfort and well-being to the animals. The supply of shade at the

Table 2 Main physical changes in the environment, nutritional strategies, and genetic selection to mitigate heat stress in cattle

Breed	Gender	Factor	Geographic location	Main outcomes	Authors
Angus	Male	Effect of shading on performance and welfare	Australia	Shade access reduces the heat load, improves weight gain, increases dry matter intake, and welfare of Angus steers in a feedlot system.	Gaughan et al. 2010b)
Holandês Friesian	Female	Shade provision	New Zealand	Shading provision for dairy cattle raised on pasture improves the physiological condition, reducing the respiration rate and preventing an increase in rectal temperature.	Schutz et al. (2010)
Holstein	Female	Convective cooling	USA	The benefit of cooling dairy cows with a fan depends on the air temperature and the body surface temperature; this mechanism is more efficient during the night.	Spiers et al. (2018)
Italian Friesian	Female	Forced ventilation combined with fogging	Italy	The use of fans combined with nebulizers neutralizes the adverse effects of heat stress, helping animals to be more efficient in dissipating heat and improving their body temperature regulation.	Calegari et al. (2016)
Holstein	Female	Cooling on the heat-stressed dairy cows	USA	The benefit of cooling cows under heat stress during the dry period was observed with an increase in milk yield during posterior lactation.	Tao et al. (2012)
Canchim	Female	Effects of microclimate on integration systems	Brazil	The crop-livestock-forest system improves the environmental conditions of the pastures, providing a more favorable microclimate for thermal comfort of the cattle, due to the shading from trees, reducing the body surface temperature.	Giro et al. (2019)
Holstein, Senepol	Female	Smooth haircoat phenotype and thermoregulatory capacity	USA	Holstein cows crossed with the Senepol breed inherit the smooth hair gene and consequently have an easier time regulating body temperature due to increased sweating capacity.	Dikmen et al. (2014)
Angus, Brahman	Female	Influence of Brahman genetics on the Angus herd	USA	The cross between $^5/_8$ Angus + $^3/_8$ Brahman leads to a reduction of 0.3 °C in the rectal temperature of the F1 animals.	Dikmen et al. (2018)
Holstein	Female	Saturated fatty acid supplementation	China	Saturated fatty acid supplementation reduced the maximum rectal temperature of cows under heat stress, besides improving milk production and milk fat content.	Wang et al. (2010)
Holstein	Female	Chromium supplementation	Iran	Calves supplemented with chromium during the summer had their lower respiratory rates and improved growth and feed intake, besides reduced heat stress.	Kargar et al. (2018)
Holstein	Female	Radix Bupleuri extract supplementation	China	*Radix Bupleuri* extract supplementation reduces the rectal temperature of Holstein dairy cows, a feeding strategy to mitigate the heat stress effects.	Pan et al. (2014)

disposal of animals can reduce the heat load that comes through direct solar radiation by up to 45% (Kamal et al. 2016).

Solar radiation and air temperature are the two main meteorological variables that directly influence the thermal comfort of cattle (Berman 2019). Seeking solutions to protect animals from these stressors is critical for providing an ideal (or near) environment to maximize animal productivity. Fans, evaporative cooling, water sprinklers, and shading (natural or artificial) are the most common strategies used to modify cattle farming environments (Scholtz et al. 2013; Henry et al. 2018; Berman 2019). The implementation of closed production systems equipped with fans and sprinklers to improve heat loss by evaporative cooling, as recommended for Holstein dairy cows (Calegari et al. 2016), has become unviable for systems of production predominant pasture in countries like Brazil. Providing shade in adequate quantities serves as a barrier against solar radiation, reducing heat load and air temperature, and improving animal welfare (Karvatte et al. 2016).

The implantation of a movable shade in a pasture system for dairy cows appears to be an alternative to the intensive production systems verified by Palacio et al. (2015), demonstrating satisfactory results for the thermal comfort of animals. Shadow structures in confinement can bring benefits like greater beef production, in addition to reducing direct solar radiation exposure (Gaughan et al. 2010b). Sullivan et al. (2011) observed that Angus cattle in confinement gain an extra 11 kg of final weight when they have access to 2.0 m^2 of artificial shade unlike animals that did not have access to shade. The use of shades has been increasingly sought after as a quick and efficient strategy to promote shade in animals. In addition to speed, shades also promote a more favorable microenvironment for animals than materials such as asbestos roofing tiles (Kamal et al. 2014).

Several studies have been conducted on forest-farming-livestock integration systems (Karvatte et al. 2016; Lopes et al. 2016; Pezzopane et al. 2019; Giro et al. 2019). Karvatte et al. (2016) evaluated three types of integration-farming livestock–forest systems and found that there was a significant reduction of 28.3% in the radiant thermal load in shade compared to that under full sun exposure, indicating an improvement in the thermal environment, especially when native trees are dispersed or when eucalyptus trees are used at a lower density per area.

The possibility of cooling cows during the pre-birth period may be a strategy to increase daily milk production. In experiments conducted by Tao et al. (2012), it was observed that the cows of the Holstein breed that passed the pre-delivery period in the free stall with sprinklers and fans produced 6.3 kg milk/day higher than the cows that were housed in a free stall with only a shade. In the same study, the authors also found that the cooled cows had a rectal temperature of 38.55 °C and respiratory rate of 48.3 breaths/min, while the cows that were not cooled had a rectal temperature and respiratory rate of 39.34 °C and 69.2 breaths/min, respectively. Calegari et al. (2016), studying evaporative cooling (nebulizers in the resting area) in dairy cows of the Friesian breed during the Italian summer (July to September), observed that the cows had an average respiratory rate of 55.8 breaths/min, which was lower than that of cows that were housed in the resting area only with ventilators (60.2 breaths/min).

Selection of heat-tolerant genes

Genetic selection for heat tolerance in cattle has been occurring with great intensity in recent years to better understand the mechanisms of heat resistance and to seek better adapted and productive animals according to production systems (Henry et al. 2012; Osei-Amponsah et al. 2019). A key objective for using animals adapted to heat-adverse conditions is their ability to survive in stressful environments (Osei-Amponsah et al. 2019). The use of Zebu breeds crossed with taurine breeds has been a way to extract the best of the two subspecies: the heat tolerance of Zebu cattle (Cardoso et al. 2015) and the productivity of *Bos taurus* cattle, boosting productivity in the hottest regions (Henry et al. 2018).

The identification of thermotolerant alleles is a strategy used to target mating in livestock. According to Taye et al. (2017), heat shock proteins (HSP's) are associated with the response to thermal stress, with an increase in thermotolerance being verified through their functioning as molecular chaperones (Gupta et al. 2013; Belhadj Slimen et al. 2015). The cattle, mainly the zebu, can present high tolerance to thermal stress in tropical climate environments. This resilient capacity is due to a lower metabolic rate expression and body temperature regulation (Taye et al. 2017). Genetic selection as a strategy to mitigate the effects of thermal stress is time-consuming and cumulative because genetic improvements are not lost; however, genetic evaluation using mixed models (Schaeffer 2014) associated with genomic evaluation can leverage the selection of superior animals for heat tolerance and favorable characteristics that meet market specifications (Gaughan et al. 2009; Renaudeau et al. 2012; Taye et al. 2017). According to Dikmen et al. (2014), the crossing of Holstein cows with the Senepol breed may allow the progeny to inherit the SLICK haplotype, thus improve thermoregulatory capacity. This leads to a lower RR and RT following a higher sweating rate throughout the day as well as greater milk production unlike in cows that do not have the SLICK haplotype.

The introduction of Zebu cattle genes in taurine cattle has become a way to optimize the adaptation of future progeny to thermally adverse conditions, where it is necessary that at least 25% of the cross corresponds to Zebu genetics to have some adaptive effect and between 50 and 75% for more extreme climate and feed conditions (Dikmen et al. 2018). In studies by Dikmen et al. (2018) with Angus and Brahman cows, the body temperature of Brahman cows was 38.5 °C at the hottest times of the day, while Angus cows were 40.0 °C, with a difference of 1.5 °C between breeds at the same time. Contrastingly, in the cross between these two breeds resulting in a $^5/_8$ Angus + $^3/_8$ Brahman animal, the vaginal temperature difference was around 0.3 °C compared to that of pure Angus animals, conferring that crossbreeds can be used to improve tolerance to stressful thermal conditions.

Thus, we observed that the adaptive capacity of animals tolerant to thermally stressful environments and deficient nutritional resources, along with disease resistance and tolerance (Hoffmann 2013), can be useful as long-term strategies for maintaining or maximizing productivity (Gaughan et al. 2010b).

Nutritional manipulation for heat stress mitigation

In hot climate regions, animals tend to decrease feed intake to regulate metabolic heat production (Sejian et al. 2018). Min et al. (2019) pointed out that several nutritional strategies should be evaluated to alleviate the impact of thermal stress, such as altering fat, vitamin, mineral, and fiber levels in the diet to maintain animal performance. Renaudeau et al. (2012) also highlighted strategies for water intake by animals.

Water consumption

Water consumption is essential for animals in any geographical region, especially when exposed to thermal stress. In hot climates, the consumption increases. It is vital to provide good quality and abundant water so that animals do not suffer water restriction (Renaudeau et al. 2012) and preferably close to shaded places with the intention of maintaining the water temperature for animal consumption. The water intake of Holstein cows with 28 kg milk/day can vary from 121 to 135 L per day under thermally stressful conditions (Hall et al. 2016).

Dietary fiber

Dietary fiber digestion results in high heat production from ruminal fermentation and nutrient metabolism (Baumgard et al. 2014). Manipulating the quantity and quality of fiber in the diet has been studied as a way to reduce metabolic heat production and mitigate the effects of thermal stress through diet (Gonzalez-Rivas et al. 2018; Min et al. 2019). Corn silage substitution with beet pulp of up to 12% in the dry matter of the diet may favor Holstein cows to breed under moderate thermal stress, where better fiber digestibility provides less ruminal filling and consequently reduces the metabolic heat production in the digestion process (Naderi et al. 2016).

Lipids

Several researchers have verified that animals in warm climates have reduced dry matter intake (Gaughan et al. 2010b; Blaine and Nsahlai 2011; Curtis et al. 2017), leading to a decrease in their performance. Lipids present a lower caloric increase than carbohydrates in energy metabolism (Renaudeau et al. 2012). To alleviate the problem of lower dry matter intake in hot environments, adding lipids in diets increases energy density, reduces heat stress signals, and improves feed efficiency and performance (Melo et al. 2016). The partial replacement of corn in the diet with 1.5% saturated fatty acids reduced the rectal temperature by 0.81 °C when the air temperature was 30°C and increased milk production by 2.2 kg in Holstein-bred cows unlike in cows that did not receive dietary oils (Wang et al. 2010).

Minerals

Oxidative stress, which can be caused by heat stress, has a negative impact on animal physiology and metabolism. It induces an increase in free radical formation and reduces the antioxidant capacity of animals (Zhang et al. 2014; Das et al. 2016). To improve the antioxidant defense system of animals, trace minerals such as selenium have been studied for its potential in reducing reactive oxygen species production, which are harmful to animals (Calamari et al. 2011; Gong and Xiao 2016; Oltramari et al. 2014; Min et al. 2019).

Minerals and vitamins play key roles in animals. However, in response to thermal stress, it is believed that heat loss increases mineral excretion (Min et al. 2019). Chromium supplementation in the diet of calves improves thermal stress reduction, with a significant decrease in respiratory rate and a slight decline in rectal temperature (Kargar et al. 2018). Supplementation of Holstein cows with 6 mg chromium per day up to 8 weeks postpartum decreased cortisol levels to 2.91 μg/dL, whereas postpartum cows that were not supplemented with chromium had cortisol levels of 3.59 μg/dL. Supplemented cows had an average milk production of 3.7 kg, which was higher than that of the non-supplemented cows during this period (Soltan 2010).

Vitamins

According to Min et al. (2019), adding vitamins to dairy cow diets can mitigate the adverse effects of thermal stress. In the experiments of Bordignon et al. (2019), Holstein calves supplemented with vitamin E had lower oxidative stress levels, lower respiratory rate, and a higher body rate at the end of a 45-day experiment than calves that were not supplemented. In high-producing cows (38.2 kg/milk/day), supplementation of 12 g/cow/day of encapsulated niacin (vitamin B_3) led to a 0.4 °C reduction in vaginal temperature, possibly due to increased vasodilation and changes in blood flow to peripheral tissues (Zimbelman et al. 2013).

Alternative feeds

Alternative feeds have been widely studied as an option using traditional concentrates and forage. The antioxidant potential of alternative feeds such as moringa (*Moringa oleifera*), oregano (*Origanum vulgare*), cinnamon (*Cinnamomum zeylanicum*), green tea (*Camellia sinensis*), and garlic (*Allium sativum*) have been discussed as potential ingredients for reducing oxidative stress (Staerfl et al. 2011; Cho et al. 2014; Cohen-Zinder et al. 2017; Stivanin et al. 2019), which is also mainly caused by heat stress. According to Cohen-Zinder et al. (2017), the use of *Moringa oleifera* silage in the dairy cow diet has resulted in an increase of 4 kg of milk in daily production and a reduction in the somatic cell count of cows fed 270 g of silage per kilogram of dry matter per day. This verifies the promising potential of moringa in animal nutrition due to the presence of significant amounts of proteins and vitamins, and its substantial antioxidant potential. Radix Bupleuri extract, a traditional Chinese phytotherapeutic, was added in Holstein cow diet, and a reduction of 11 breaths.min^{-1} in an average air temperature environment of 31.0 °C was observed, highlighting the antioxidant potential of this phytotherapy. Furthermore, it is used as a feed strategy to mitigate the effects of thermal stress, in addition to improving dry matter consumption and consequently improving daily milk production (Pan et al. 2014).

Inclusion of alternative feeds in the diet of dairy cows under heat stress highlights their antioxidant and anti-inflammatory capacity and increases milk production. According to Lee et al. (2020), inclusion of 0.016% of combined extracts of garlic (*Allium sativum*), brown algae (*Undaria pinnatifida*), and pine (*Pinus koraiensis*) to Holstein cow diet improves the antioxidant capacity in situations of moderate heat stress, in addition to improving milk production with an increase of 1.1 L compared to that obtained with the control diet. *Origanum vulgare* strata supplementation in the diet of Jersey cows has benefitted their health, with a lower frequency of mastitis cases, improved milk production, and reduced aggressive behavior (Stivanin et al. 2019).

Final considerations

The physiology of cattle can change in response to the meteorological variations in their environment. Temperature and direct solar radiation are the main factors that negatively affect cattle physiology, making it difficult for animals to sense heat loss, causing them to spend more energy to activate the latent heat loss mechanisms. The physiological, morphological, and genetic characteristics of *Bos taurus indicus* are crucial for thermoregulatory mechanisms to maintain their physiology within the limits of homeothermy in the tropical environment. Even with a greater tolerance to tropical climate, *Bos taurus indicus* may show low performance throughout the year. In this context, several genetic, nutritional, and physical changes in the environment have been studied to understand the physiological, biophysical, and productive responses, to seek measures to ameliorate thermal stress and maximize animal production in tropical climates.

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