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THE IMPACTS OF THERMAL STRESS ON DAIRY CATTLE PHYSIOLOGY, METABOLISM, HEALTH, AND PERFORMANCE – A COMPREHENSIVE REVIEW

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Abstract

Climate change is becoming a global issue, with important implications for dairy cow performance and well-being. It is distinguished by a gradual rise in universal temperature and the risk of extreme weather occurrences. Studies have shown that heat stress (HS) impacts many biological processes that can have significant economic issues. Due to their elevated metabolic rate, cows are mostly liable to HS, which negatively affects immune function, particularly cell-mediated immune response, and subsequent reduced production performance and inferior immunity, which leads to elevated susceptibility to disease, increased incidence of intramammary infections, and an elevated somatic cell count, as well as calf mortality, particularly during the summer season. Furthermore, dry cows subjected to HS had reduced immunoglobulin levels after vaccination, although this impact fades with cooling after parturition. On the other hand, cows subjected to HS while dry demonstrate carryover impacts on the innate arm of the immunity in early lactation, resulting in losses. Heat mitigation technologies are cost-effective and necessary for sustaining milk production and the dairy farm's profitability. Furthermore, a check of present HS mitigation measures is required to understand better and identify acceptable abatement plans for future stress management.

Key words: heat stress, thermoregulation, immune response, reproduction, dairy cattle

Climate change is currently at the forefront of many discussions in the scientific community, government, and the media (Madkour et al., 2020, 2022; Sayed et al., 2023). The rationale behind this is that it has the potential to result in several implications on the environment on a global scale, which in turn can affect the production and survival of a great number of species all over the world (Alagawany et al., 2017, 2022; Salem et al., 2022). The quantity of solar energy received by the globe and the capacity of the earth to release energy back into space are the two primary factors that define the temperature on the planet (Saeed et al., 2019; Foroushani and Amon, 2022). Heat gain and loss are mainly regulated via the thermoregulation mechanism as heat flows from warmer to cooler surface to keep the normal physiological state of the dairy cattle (Sammad et al., 2020; Dos Santos et al., 2021; Correa-Calderón et al., 2022; Dovolou et al., 2023). Mammals and lactating cows must keep a relatively stable body temperature above the environmental temperature for adequate heat flow from the body to the ecosystem and to keep the core body temperature constant or within range (Collier et al., 2006 a, 2019). Usually, the cattle core body temperature is about 38°C (Collier and Gebremedhin, 2015; Uddin et al., 2021) and will remain within 1°C of this in normal ambient conditions (Berman et al., 1985; Idris et al., 2021). The thermoneutral zone could be expressed as the ambient temperature range in which an animal can keep a stable body temperature with minimal energy expenditure (Bernabucci et al., 2010; Ribeiro et al., 2020). Focusing on dairy cows, the thermoneutral zone, based on productivity measures, is an ambient temperature range from 5 to 25°C (Kadzere et al., 2002; Yan et al., 2021; Neves et al., 2022), although the optimal range for the highest efficiency in energy utilization is between 13 and 18°C (NRC, 1981; Yan et al., 2020).

Heat stress (HS) occurs when the body cannot eliminate heat excess. When this happens, the body's core tem-

perature rises, and the heart rate increases. Exceeding the ambient temperature over an animal's thermoneutral zone means HS (Buffington et al., 1981; Purohit et al., 2020). When the surrounding temperature moves over the maximum critical threshold, thermoregulatory mechanisms can no longer compensate for heat gain, causing the body temperature to rise (Bernabucci et al., 2010; McKechnie, 2022). This zone can vary in dairy cows depending on their age, breed, production, ration, previous temperature acclimatization, coat color, and amount of tissue insulation (Kadzere et al., 2002; Krishnan et al., 2023).

Metabolic heat liberation can differ significantly among dairy cattle during the production cycle, affecting the cow's capability to emit heat (Dahl et al., 2020; Sammad et al., 2020); A cow weighing 600 kg produces about 40 kg of milk per day with a fat content of 4%, where the distribution of intake energy was 35.3% fecal energy, 5.3% gaseous energy, 2.8% urinary energy, 25.5% lactation energy and 31.1% heat production (Coppock, 1985), as shown in Figure 1.

The HS is heat acquired from the environment and the disaster to disperse heat combined with production activities (West, 2003; Navas-Martín et al., 2024). Lactating animals could generate heat significantly higher than a non-lactating dairy cow of similar weight (Nardone et al., 2006; Valencia-Franco et al., 2024). A study of non-lactating, low-intermediate milk production (18.5 kg/d) and intermediate-high milk production (31.6 kg/d) dairy cattle revealed the low and intermediate dairy cattle could produce more heat (27 and 48, respectively) than that originating from the non-lactating one (Purwanto et al., 1990). As a result, during HS, the energy required for upkeep rises owing to the energy-demanding manner of heat dissipation, as the cow's capacity to disperse heat is critical to tolerate HS (Kovačić et al., 2022; Shephard and Maloney, 2023). Also, core body temperature rises due to changed metabolic processes, dry matter intake, and digestion, all necessary to promote a high milk supply (Correa-Calderón et al., 2022; Pontiggia et al., 2024).

Scientists demonstrated that HS during early lactation can hurt the milk yield, as the milking stage is associated with HS tolerance, where cattle in early lactation appear less tolerant to HS than those in the late season (Sharma et al., 1983; Moore et al., 2023; Mylostyvyi et al., 2024). This might be related to negative energy balance, a frequent occurrence in early lactation as they mobilize cell stores to counteract an energy shortage caused by the energy-demanding for milk yield. Furthermore, cattle with a negative energy balance have restricted energy to maintain thermoregulatory mechanisms.

Thermoregulation and production

The body heat from the ecosystem is utilized to keep the animal's temperature stable. So, any excess heat for this demand is dispersed to the ecosystem by thermoregulatory mechanisms (Berman, 2011; Lahondère, 2023). There are several ways of thermoregulation via which homoeothermic dairy cows may gain and lose heat, such as conduction, convection, radiation, and evaporation. It impacts the cows' thermoregulation capacity during HS, as shown in Figure 2.

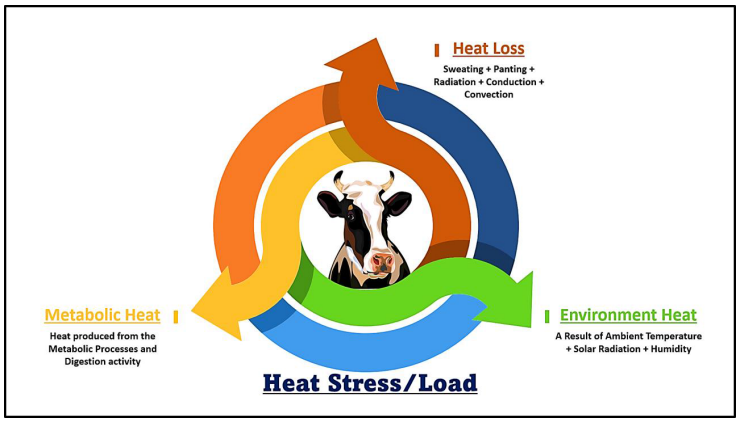


Figure 1. Heat sources in the dairy sector implemented in the heat stress

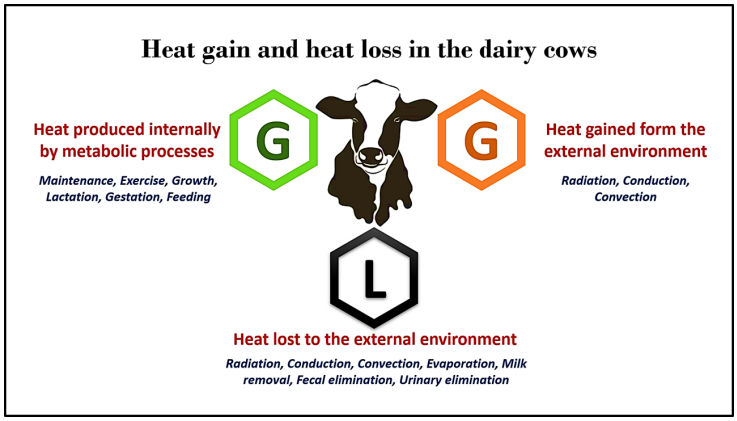


Figure 2. Heat gain and heat loss in the dairy cow ecosystem

Thus, lactating dairy cows have a higher rectal temperature than non-lactating cows at thermoneutral settings and a Celsius higher rectal temperature than prepartum pregnant dry cows (Shalit et al., 1991; Becker et al., 2020; Cartwright et al., 2023). The magnitude of HS or thermal tolerance makes lactating cattle more vulnerable to HS than non-lactating ones. This may be because of a diminished capacity to keep plasma volume within a restricted physiological range. As a result, the intensity of HS experienced by dairy cattle seems to depend on milk output and lactation stage (Cartwright et al., 2023). The main reason for increased metabolic heat generation is the large amount of feed necessary to sustain milk synthesis, which reduces the range of climatic circumstances under which an animal can lose heat at the same rate as it accumulates (Gross, 2022; Lourencon et al., 2024). Ration-wise, the concentrate/forage ratio in the dairy cow ration has been changed to adapt and acclimatize their HS tolerance by minimizing the forage consumption (Bernabucci et al., 1999), where this decrease in fiber consumption would lower the heat produced during digestion and is thought to be an adaptive behavioral reaction to HS.

Thermoregulation mechanisms

Broadly, thermoregulation mechanisms involve three pathways that link the external environment to thermoregulatory responses: the afferent pathway, the central nervous system (CNS), and the efferent pathways (Collier and Gebremedhin, 2015). The afferent pathway involves transient receptor potential (TRP) ion channels in the skin that detect environmental temperature (Collier and Gebremedhin, 2015). These TRP ion channels have different thermal activation thresholds, such as heat, warm, and cold-activated channels (Numata et al., 2011). Activation thresholds of different warm TRP ion channels range between 31 and 39°C, 25 and 33.6°C, and 15 and 35°C. At the same time, specific thresholds have not been described for dairy cows, while humans have a heat-activated TRP ion channel with an activation threshold of 42°C (Numata et al., 2011; Collier and Gebremedhin, 2015).

Information is transmitted from TRP ion channels via sensory neurons in the spinothalamic pathway to the central nervous system (Collier and Gebremedhin, 2015); firstly, the thalamus receives this sensory information and transfers it to the hypothalamus, and the cerebral cortex enables the thermal perception, as well as the hypothalamus, activates the sympathetic nervous system and endocrine system for thermoregulatory responses. Thermoregulatory mechanisms involve cardiovascular changes, behavioral responses, metabolic responses, and endocrine responses. Increased body temperature will cause vasodilation of the skin's blood vessels, sweat production from sweat glands, lowered metabolic rate, and reduced activity and appetite as a behavior change (Collier and Gebremedhin, 2015). Heat exchange (thermal tolerance) comprises four pillars: radiation, conduction, convection, and evaporation (Tansey and Johnson, 2015). Briefly, radiation occurs when heat is transferred between bodies not in contact, such as ultraviolet (UV) light from the sun and infrared (IR) radiation from the body. Conduction is the heat transfer between objects in contact, and convection is when air molecules in contact with an object are heated, and heat is transferred away from the object in a gas or liquid (such as the movement of air over an object). Evaporative means heat transfer occurs when heat is lost as water vapor from the respiratory system and skin, as shown in Figure 3.

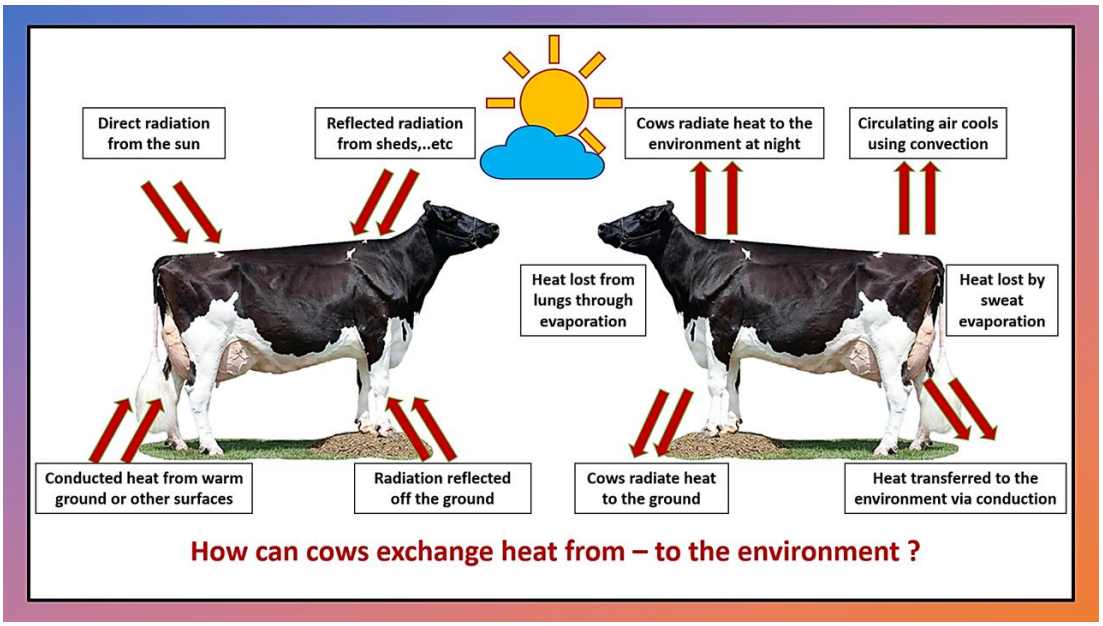


Figure 3. Heat gain and heat loss from and to the cow in the farm

Dairy cows can interact with their thermal environment through peripheral thermoreceptors and thermoregulation (convection, conduction, radiation, and evaporation), primarily determined by ambient temperature; where ambient temperature rises, heat loss shifts from convection and radiation to evaporation (Yousef and Johnson, 1966; Kadzere et al., 2002). It was discovered that many kinds of temperature-sensitive neurons in the hypothalamus detect temperature alterations and then activate heat loss or heat gain processes. Also, thermoreceptors in the encephalon and integument communicate with the hypothalamus. HS stimulates the anterior hypothalamus, which commences heat dissipation processes, and cold stress activates the posterior hypothalamus, which initiates heat gain mechanisms (Wit and Wang, 1968; Bohler et al., 2021; Krishnan et al., 2023). The quantity of radiant heat an animal acquires is influenced by its coat color; hence, an animal with mostly black skin would absorb higher heat than an animal with a predominantly white coat.

Conduction

The heat transfer process that occurs when an animal's surface comes into contact with another substance, often solid, is called conduction (Schmidt-Nielsen, 1964). The temperature difference between the two substances that are in touch, the area of contact, and the thermal conductivity of the temperature difference between the two substances are all factors that influence the exchange of heat by conduction (Schmidt-Nielsen, 1964). Conduction is often a very insignificant part of the heat exchange process while an animal is standing; however, it can become a significant part of the process when an animal is lying on the ground (Macfarlane et al., 1958). In cattle, the ground is the primary medium through conduction. As a result of the fact that the rate of heat transfer through conduction is dependent on the area of contact, the rate of heat transfer into the colder ground is higher when cattle are lying down as opposed to when they are standing (Yousef, 1985). Animals lying down tend to have a lower rectal temperature than standing animals but a greater cutaneous temperature (Macfarlane et al., 1958).

Convection

Convection is the transfer of heat due to the bulk movement of molecules within fluids. For cows, this primarily involves heating (and removing) the air around the body. The body is subsequently surrounded by cool air, and the procedure is frequent (Silanikove, 2000). Dilation of blood vessels, as a physiologic reaction to HS, uses this heat dissipation strategy by drawing more blood to the integument and boosting blood flow. This enables a higher integument surface temperature to offload heat to the air via the heat gradient (IPCC, 2007).

Radiation

Radiation heat up taken by an object is mainly affected by its temperature, color, and texture (Kadzere et al., 2002). According to statistics, a dairy cow with black skin may grasp 2.7-fold more radiant heat than an animal with a white coat (Cena and Monteith, 1975). Darker coat dairy cows have a higher absorption capacity, negatively influencing production performance and adaptation. Lactating dairy cattle with more than 70% white pigment had reduced body temperature and higher milk output than cattle with more than 70% black pigment. Furthermore, dairy cows subjected to radiant heat in a facility with no shade reduced milk output by an average of 1.5 kg/24 h in white cattle and doubled to 3.3 kg/24 h in black cattle (Hansen, 1990). Also, dark-coated *Bos taurus* beef cattle had increased heat transmission to the integument, greater body temperature, and lower weight increases than white-coated cattle (Finch, 1986).

Evaporation

Moisture evaporating from the integument, or the respiratory system, requires heat to change the water to its gaseous form, cooling the blood circulating in the dilated blood vessels underneath the integument surface. When air temperature exceeds integument temperature, evaporative heat dispersal is the most efficient type of heat loss (Kibler and Brody, 1952 b). Many interconnected elements influence evaporative heat dissipation, including accessible skin surface area, wind speed, air temperature, and humidity (Silanikove, 2000). Evaporative heat loss is a very effective procedure at high air temperature and low relative humidity (RH) (Silanikove, 2000), which acts as an insulator from evaporation and heat loss.

Panting is an alternate method for heat loss by conduction that appears as increased respiratory frequency, resulting in increased carotid blood flow to the nasal mucosa, carrying cooled blood and lower brain temperature. Similarly, panting induces respiratory thermal loss by increasing blood flow to the tongue. The cooling action of the nasal mucosa and the tongue has been found to lower carotid artery and jugular vein temperature during open-mouth panting (Blix et al., 2011).

Assessing HS

Fever in dairy cattle happens when the rectal temperature moves beyond 39°C. Thus, direct measuring body temperature is the most accurate tool for measuring HS (De Rensis et al., 2015), but it is not always the most feasible (Dikmen and Hansen, 2009). In practice, the temperature-humidity index (THI) (West, 2003) is often applied to measure the danger of HS in dairy cattle, which was initially devised by Thom (1959), as shown in Figure 4.

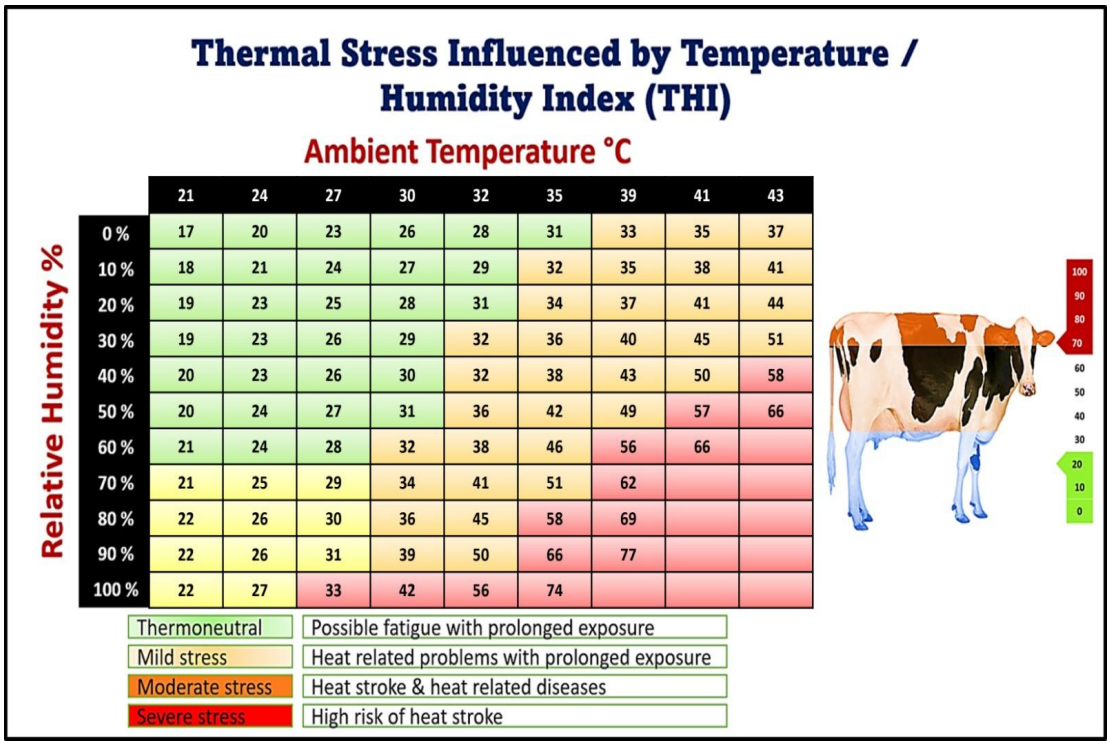


Figure 4. Correlation between heat stress and different temperature/humidity (THI) for the dairy cattle

The THI is a value that represents air temperature and relative humidity (RH) (Bernabucci et al., 2014). Consequently, solar radiation and wind speed can affect HS (Buffington et al., 1981). Many kinds of literature declare the THI different calculation formulae as THI = (1.8 × air temperature in °C + 32) – [(0.55 – 0.0055 × RH in %) × (1.8 × air temperature in °C – 26.8)] (NRC, 1971) and THI = (0.8 × air temperature in °C) + [(RH in %, 100) × (air temperature in °C – 14.4)] + 46.4 (Mader et al., 2006), and is often classified into different zones to depict when HS begins. Owing to the formula, HS is thought to start at the index of 68 (Zimbelman et al., 2009 a; Ferreira et al., 2016) or 72 (Armstrong, 1994). A THI of 72 equates to approximately an ambient temperature of 25°C at an RH of 50%. So, THI measures were used as mean, minimum, and maximum h above a specific value and can also affect the results of studies on HS in dairy cows (Collier et al., 2011).

Many studies have identified different thresholds when HS begins, e.g., mean THI = 72 (Igono et al., 1992); several hours per day with a THI >74 (Linvill and Pardue, 1992); mean THI >60 (Brügemann et al., 2012); maximum THI between 65 and 76 (Bernabucci et al., 2014); mean THI >68 (Zimbelman et al., 2009 b) or different ways of calculating THI that are most associated with HS effects on dairy cows with minimum temperature (Holter et al., 1996) or with maximum temperature and minimum RH (Ravagnolo and Misztal, 2000). Literature has suggested that HS may best be characterized by including THI measures of previous days, as opposed to just the day of interest 2 days (West et al., 2003); 3 days (Bouraoui et al., 2002; Hill and Wall, 2017); 2–4 days (Spiers et al., 2004) or 4 days (Linvill and Pardue, 1992). Therefore, other physiological factors such as rectal or vaginal temperature, respiration rate, sweating, panting, feed intake, standing period, and activity are often applied to evaluate HS (West, 2003; Schütz et al., 2008; Hansen, 2013), as shown in Figure 5.

Physiological responses to thermal stress

A lag in response to elevated ambient temperature is logical and provides a time for behavioral and physiological responses (West et al., 2003). In feedlot cattle, increased rectal temperature lags 4–5 h after ambient temperature changes, and increased respiratory rate lags 1.5–2 h (Brown-Brandl et al., 2003). The vaginal temperature in dairy cattle has been indicated to lag two hours behind changes in THI (Kendall et al., 2006). For periods of prolonged heat load, Hahn (1999) suggested that approximately 3 to 4 days are required for cattle's thermoregulatory mechanisms to reduce metabolic heat formation, which helps the animal to overcome thermal stressors (Kadzere et al., 2002).

Normal physiological functioning requires thermoneutrality (Kadzere et al., 2002). Consequently, dairy cattle have a wide range of sensitivities to environmental circumstances above the thermoneutral zone. Even though the physiological reactions of dairy cows to HS seem to be breed-specific, these responses can be summarized as elevated rectal temperature, elevated respiration, panting, excess sweating, salivation, and water intake, but lower feed consumption, milk yield, and heartbeat (Kadzere et al., 2002).

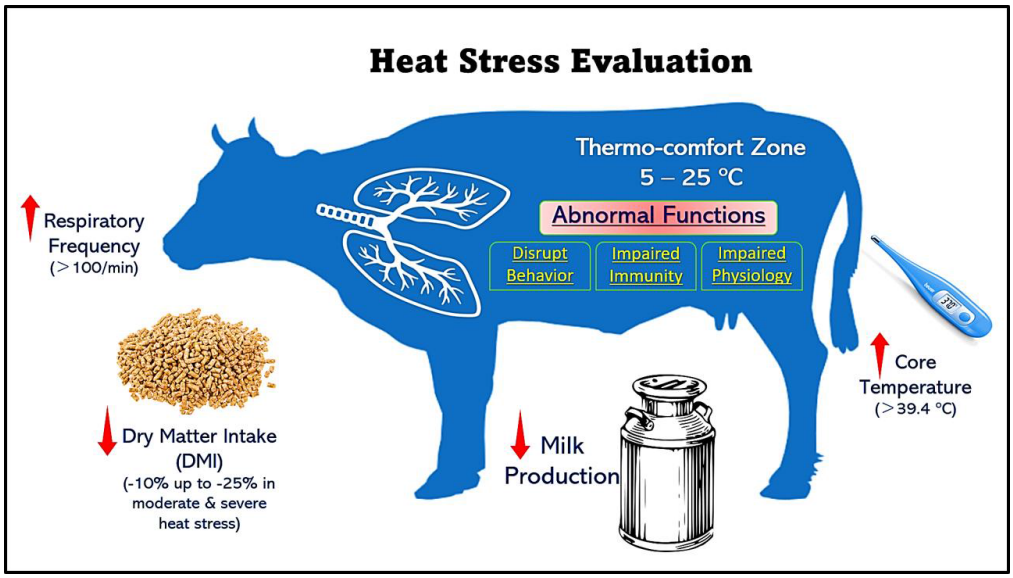


Figure 5. Evaluation of the heat stress in dairy cattle

Despite wide fluctuations in ambient temperature and when heat gain is greater than heat dissipation, homeothermic dairy cows can maintain a relatively constant body temperature through compensatory increased respiratory rate to improve evaporative heat loss strategy (Bouraoui et al., 2002; Beatty et al., 2006). This capacity to maintain body temperature within a small range is critical for preserving the biochemical reactions and physiological processes involved in proper homeostatic metabolism.

Temperature-sensitive neurons are found in cows' bodies and provide data to the hypothalamus in the encephalon. In extreme HS situations, the body's temperature is not maintained, which represents the body's core temperature. Physiological self-preservation systems are activated to sustain the unique situation of homeostasis; however, this comes at the expense of cow production. Because milk synthesis and secretion are sources of metabolic heat generation (Fan et al., 2019), and HS alters the hormones essential for proper ovarian function (as HS does), milk yield and reproduction are particularly sensitive to variations in body temperature (Wolfenson and Roth, 2019).

Body temperature

Integument temperature is an available metric since it may be obtained from a distance and does not require restraint or restriction of the animals' mobility. Rectal temperature is kept constant under normal situations via thermoregulation, which means that rectal temperature may be utilized as an accurate key indication of thermal load (physiological HS) reactions. A Celsius degree difference in rectal temperature is sufficient to impair cow health status and productivity (McDowell et al., 1976). Because of its great association with rectal temperature, vaginal temperature might potentially be utilized as an indication for HS (Vickers et al., 2010). Vaginal temperature is monitored by temperature sensors that provide estimations of core body temperature 24 h a day (Vickers et al., 2010; Rutten et al., 2017). This measuring procedure enables the characterization of daily patterns in core body temperature, which are influenced by external variables (Collier et al., 2006 a).

Respiration

The respiration rate is an essential indicator of the degree of HS in dairy cattle. Cows lose heat by evaporation when air travels across the top respiratory process, transmitting heat from the bloodstream to the air and subsequently breathed (Zeng et al., 2023). Exposure to HS negatively impacts dairy cows' lactation performance and health status by limiting oxygen transportation and metabolism (Zeng et al., 2023). For every one ml of H_2O evaporated from the respiration, approximately 2.43 J of heat is missed to cool the blood running via the underlying areas' respiratory tissues (Silanikove, 2000). On the other hand, sheep lose roughly 20% of their entire body heat through respiration, which can reach 60% during HS (Marai et al., 2007).

During thermoneutral circumstances, the usual respiratory rate for dairy cattle is around 20 breaths per minute; however, when temperature and humidity rise, the respiratory rate climbs to roughly 60 breaths per minute at air temperatures over 25°C (Berman et al., 1985, Radostits, 2007) up to over 90 respirations per minute with THI over 90. When the air temperature goes over the body temperature, respiration is considered a critical process for heat loss "evaporation"; as the respiratory rate elevates, the quantity of water also lost rises, and heat is lost from the body where the water lost from the respiration is noticed to be elevated from 1 to 2.9 L in 24 h as temperature increases from 28 to 38°C (Blaxter et al., 2009). However, as humidity rises over the humidity gradient, heat loss efficiency by evaporation suffers greatly

(Coppock et al., 1982). Another important issue resulting from an over-respiratory rate is the respiratory system's pH change reflected in the blood pH and, consequently, a normal physiologic state (Coppock et al., 1982).

Sweating

In the dairy cow, there are two types of sweating: insensible perspiration and thermal sweating, which are included in heat dissipation. Except when RH is 100%, insensible sweat continually exits the body. The second kind is thermal sweating, when the air temperature rises above the integumentary temperature, triggering evaporative cooling (Allen et al., 2015; Dourmad et al., 2022).

The number of sweat glands per unit surface area of integument varies by breed. Zebu cattle, for example, have much more sweat glands than Friesians (Dowling, 1955). Nevertheless, Blazquez et al. (1994) determined that the count of sweat glands per unit of integument surface area is not relevant but rather the cumulative functional characteristic of sweat-producing glands. Allen (1962) discovered breed variations in sweating ratios as ambient and integument temperatures rose. Jersey heifers sweated linearly as skin and air temperature rose, but zebu heifers did not sweat until their skin temperature reached 35°C. The sweating rate is also connected to skin and hair, and calves with a slick coat sweat more during HS than wild-type cows. As a result, slick-haired cows have higher thermoregulation abilities (Dikmen et al., 2008).

Blood biochemical changes

Blood pH should be maintained inside normal physiological ranges to preserve homeostasis during HS. Blood pH is primarily determined by the amounts of carbonic acid and basic bicarbonate (Coppock et al., 1982). Blood pCO_2 and HCO_3 levels were lower in thermal-stressed dairy cows compared to thermoneutral lactating cattle (Schneider et al., 1988). So, cattle exposed to HS periods had higher blood pH than thermo-neutrals. It was also found that dairy cows adjusted for respiratory alkalosis under HS by raising urine pH relative to urine pH during colder times, and blood HCO_3 concentrations decreased (Schneider et al., 1988). The commencement of hyperventilation induced by temperature stress lowers the pCO_2 level, and excess HCO_3 is eliminated through the kidneys to maintain homeostasis and relieve respiratory alkalosis.

The HCO_3 buffering approach is the most critical as it keeps HCO_3 and pCO_2 at an almost stable ratio of 20:1. Thermal-stressed cattle were excreting H^+ in urine, as evidenced by decreased urine pH and greater urine ammonium contents during colder hours, and H^+ elimination resulted in resorption of HCO_3 by the blood because of the modifications to counteract pulmonary alkalosis (Schneider et al., 1988).

Digestive tract

HS affects the digestive system and feeds the digestion process of dairy cows, which can have a negative impact on the dairy industry; where it affects the passage rate and digestibility of feed in dairy cattle as the rates of liquid and solid digestion would slow down contrasted to thermoneutral cattle (Schneider et al., 1988). Despite non-affected percentages of acetate and propionate, the concentration of volatile fatty acids (VFAs) was reduced by 9.1% due to weaker liquid dilution and slower transit rate in response to HS.

A crucial point concerning HS is the effect on the rumen temperature, which is considered a driver for appetite regulation, and the pernicious effect on the rumen flora and fauna. Consequently, the feed intake will be reduced by about 15% (Gengler et al., 1970). So, cattle supplied with chilled drinking water raised feed consumption by 24% and lowered rectal temperature (Bhattacharya and Warner, 1968). In addition to the passage rate and digestibility of feed in the digestive tract of dairy cows, the digestion of dry material in the feed is elevated during hot circumstances, owing to decreased dietary intake and a slower transit rate. As a result, variations in food digestibility may indicate an adaptive response to long-term HS. Furthermore, dairy cows modify their concentrate/forage ratio intake under HS as fiber intake decreases, affecting the passage and digestion rate (Bernabucci et al., 1999). This adaptive behavioral reaction to HS would lower metabolic heat output from digestion (Bernabucci et al., 1999).

Immunity and its role

HS is one of the most challenging risks to the immune system, from the structure to the action level, and is considered one of the most important immunosuppressive factors affecting the entire dairy system by impairing the immune system functions, which may be attributed to the decreased migration of leukocytes to the mammary gland (Elvinger et al., 1992; Cartwright et al., 2021). On the cellular level, HS influences immune system function as an acute alteration by promoting the creation of what is known as "heat shock proteins" (HSP) due to changes in gene expression that affect the entire tissues and immune system as well (Salak-Johnson and McGlone, 2007; Bett et al., 2017).

The functions of the HSP produced under temperature stress are mostly linked with the endocrine system. However, it also operates at an extracellular concentration by stimulating innate immunity, the initial line of defense versus microbial attack (Collier et al., 2008). One of the first physiological activities linked with the HS-induced rise in HSP70 expression is gained thermotolerance, which is the cell's capacity to tolerate HS following prior sub-lethal HS (Kregel, 2002). The severity and time of the first heat exposure impact the manifestation of thermotolerance.

HS-related health concerns may be caused by the reduced immunological function reported in heat-stressed dairy calves. HS can influence both the innate and adaptive immune systems. HS disrupts the equilibrium between T-helper 1 (TH1) and T-helper 2 (TH2) responses,

inducing a shift toward a TH2 response (Salak-Johnson and McGlone, 2007). This bias may hinder cell-mediated immune response (CMIR). HS has also been demonstrated to inhibit lymphocyte proliferation and population in dairy cattle (Bhanuprakash et al., 2016; Bagath et al., 2019). Bovine lymphocytes cultivated *in vivo* showed a 14-times rise in HSP70 production in interaction with HS at 42°C ambient temperature (Guerriero and Raynes, 1990). Peripheral blood mononuclear cells collected from dairy calves exposed to circumstances larger than THI 72 exhibit reduced proliferation *in vitro* in reaction to mitogenic effect contrasted to animals subjected to situations lower than THI 72 (Lacetera et al., 2005). Lymphocytes, which contain B and T cells, multiply fast in response to invading pathogens to ease clearance. As a result, lower lymphocyte proliferation makes it more difficult for cattle to defend against invading infections.

Another crucial immune system defense mechanism is the synthesis of chemicals that kill or harm pathogens. Nitric oxide is a chemical that plays a vital function in pathogen defense (Schairer et al., 2012). Furthermore, nitric oxide has been identified as a chemical contributing to thermotolerance in ruminant species (Yadav et al., 2016; Sejian et al., 2018). This is most likely because nitric oxide plays a vital role in the vasodilation of cutaneous blood vessels under HS (Kellogg et al., 1998). As a result, nitric oxide plays a function in infection defense and may also play a key part in protecting dairy cattle from the detrimental effects of HS.

Several pillars in the dairy industry have been placed at the top of the profit margin, including immune response, passive transfer to calves, and hoof health. Dairy cattle with strong immune responses appear to help their calves by passing on their high immune response genetics and giving colostrum with elevated total immunoglobulin-G and ß-lactoglobulin levels (Fleming et al., 2016). High-immune responding cattle have a lower disease occurrence and are more responsive to commercial vaccines than animals classified as low immune responders due to HS events (Wagter et al., 2000). It has also been demonstrated that strong immune responders had superior hoof health and a decreased prevalence of digital dermatitis (Cartwright et al., 2017).

Cardiovascular effect

HS and the cardiovascular system have a very close relationship because, during HS, the circulatory system transfers heat stored in the body to the body surface for offloading to the ecosystem, with the main process starting being a rise in blood flow to the skin and, as a result, the cutaneous vasodilation reaction to meet the augmented request for raised skin blood flow, as elevated heart output and heart rate is started (Pappenheimer et al., 1996). The sympathetic response, which includes sweating and the functions of adrenaline and noradrenaline, controls these effects on blood flow. The normal heart rate of dairy cattle is between 48 and 84 beats per minute.

The heart rate of lactating Friesian cows exposed to a temperature of 38.5°C with 85% relative humidity for 6.5 h during daytime and 14 to 20°C with 50 to 75% relative humidity for the remainder of each day for five weeks was 74 per minute (Richards, 1985). This elevated heartbeat is constant with the reaction to HS in cows not exposed to tropical circumstances. However, rises in heart rate are common in short-term responses to HS and diminish with long-term contact (Bianca, 2009), indicating adaptability.

Endocrine responses

The endocrine responses to HS would affect and manage other systems, including immune response and activity.

Thyroid hormones

The anterior pituitary gland produces thyrotropin and stimulates the thyroid gland's release of thyroxin (T4) and triiodothyronine (T3). These hormones govern thermogenesis and account for 50% of an animal's basal metabolic level (Beede and Collier, 1986). As a result of the HS phenomenon, there is a significant decrease in the hormones of the thyroid, which are included in the cellular absorption of glucose and, as a result, slow down the metabolic rate and heat generation, resulting in decreased feed intake and output (Silanikove, 2000; Mohammed et al., 2024). During HS, the metabolic level of dairy cattle decreases, accompanied by a reduction in thyroid hormone output.

Glucocorticosteroids

The stimulation of the hypothalamic-pituitary-adrenal axis is among the most prevalent reactions to a stressor. The motivation of the pre-optic region of the encephalon provokes the release of corticotrophin-releasing factor (CRF), which stimulates the pituitary glands to produce adrenocorticotrophic hormones. The adrenal cortex is further stimulated by adrenocorticotrophic hormone to secrete glucocorticosteroids, most notably cortisol (Smith et al., 2006). The hypothalamic-pituitary-adrenal (HPA) axis is activated, which causes an increase in plasma cortisol levels, a frequent reaction to stress (Blake et al., 1991). Glucocorticoids operate on many cells, causing physiological changes that allow an animal to adapt to its surrounding temperature at 35°C; the plasma cortisol levels of non-lactating Jersey cattle elevated within twenty minutes of acute HS, which plateaued within 2 h and returned to baseline levels 1 to 2 days post thermal stress exposure (Soliman et al., 2022). The glucocorticoid level decreases in plasma when the animal acclimates to the acute environmental heat (Christison and Johnson, 1972; Soliman et al., 2022). An increase in rectal temperature did not cause a quick rise in cortisol concentration in reaction to thermal contact because the rise in plasma cortisol level started before the increase in rectal temperature.

Prolactin

Prolactin regulates body fluids by keeping fluid outside the cells, aiding heat dissipation (Alamer, 2011). Prolactin rises with rapid alterations in ambient temperature. It has a significant seasonal connection, with the maximum and lowest concentrations happening in summer and winter, respectively, with levels increasing more than sevenfold above winter levels (Smith et al., 1977). When the ambient temperature was raised from 18°C to 32°C, prolactin levels in Holstein heifers rose more than threefold (Ronchi et al., 2001). When Holstein heifers were subjected to a temperature rise from 21°C to 32°C, prolactin levels elevated by 70% post 14 h of exposure (Wettemann and Tucker, 1976).

Growth hormone

Negative energy balance in the lactating dairy cows' plasma provokes growth hormone (GH) concentration increases. In contrast, insulin-like growth factor-1 concentration decreases, suggesting that the somatotropic axis is uncoupled during insufficient energy intake (Bauman and Vernon, 1993). An investigation on liver GH responsiveness under HS discovered that HS lowered GH receptor responsiveness regardless of decreased feed consumption (Rhoads et al., 2010).

Insulin

Inadequate calorie intake in thermoneutral settings is characterized by decreased circulating insulin (CI) or insulin tolerance (Bauman and Currie, 1980; Mohammed et al., 2023; Soliman et al., 2024). Interestingly, despite the considerable drop in calorie uptake and negative energy balance of thermal-stressed dairy animals, a rise in CI and improved insulin sensitivity is a widely observed reaction to HS (Baumgard and Rhoads, 2012). The elevated insulin concentrations are owing to elevated pancreatic production rather than decreased clearance of CI (Wheelock et al., 2010; Mohammed et al., 2022).

Metabolism

Fat metabolism

Although in a negative energy state, dairy cows subjected to extended HS do not usually mobilize fat cells stored to counteract the diminished feed consumption (Shwartz et al., 2009). This reaction is intriguing since HS raises cortisol, a powerful catabolic signal that, below normal conditions, would trigger lipolysis and fat cell mobilization (Sylvester-Bradley et al., 2005). This was described by the antilipolytic effects of HS-induced insulin level increases (Rhoads et al., 2009).

Protein metabolism

In addition to adipose tissue, skeletal tissue is mobilized during negative energy balance during thermoneutral environments to promote breastfeeding. Circulating plasma urea nitrogen (PUN) elevated by 47% during HS in nursing Holstein cattle subjected to 29 to 38°C for 21 days (Shwartz et al., 2009). PUN is derived from three resources: amino acids from the feed, a waste product of rumen ammonia creation into microbial proteins, and liver deamination of amino acids from skeletal muscle (Wheelock et al., 2010), implying that PUN level is affected by the quantity of muscular catabolism utilized as an energy resource. Creatine is another marker of muscular catabolism elevated in thermal-stressed nursing cattle (Schneider et al., 1988).

Carbohydrate metabolism

There is proof that HS affects glucose metabolism. During HS, glucose is preferentially used by other systems to increase milk production. Heat-stressed cattle have been found to eliminate exogenous glucose faster than thermoneutral controls following a glucose tolerance test (Wheelock et al., 2010). According to recent research, thermal-stressed dairy cattle release around 200 to 400 g lower lactose in milk than pair-fed thermoneutral controls. On a mole-by-mole basis, the quantity of lactose released corresponds to the amount of glucose secreted (Corazzin et al., 2020). Evidence shows that extramammary tissues use glucose more rapidly than hepatic tissue, which secretes 200 to 400 g lower glucose (Baumgard and Rhoads, 2012).

Mineral metabolism

Thermal stress modifies the mineral needs of the dairy cattle to keep homeostasis and thermoregulation and reach the required output. Specific mineral needs, such as Na^+ and K^+, change with HS. The Na^+ and K^+ electrolyte concentrations in cow ruminal fluid are lowered under HS due to elevated loss of Na^+ in urine and K^+ perspiration (Schneider et al., 1988). Milk output rose during HS in dairy cows given higher $NaHCO_3$ and KCl than suggested by the National Research Council (1989). It was also shown that feeding dairy cattle on a diet including 1.67% Cl under HS reduced blood pH, pCO_2, and urine pH compared to a control feed containing 0.34% Cl (Escobosa et al., 1984).

Water metabolism

Water (H_2O) is essential for life, and the need for water increases during HS. Water turnover is affected by dry matter intake, milk output, temperature, humidity, and respiratory-cutaneous water loss (Shalit et al., 1991; Silanikove, 1989). Water intake has a cooling impact via the reticulorumen. Higher H_2O content in the rumen can expedite the ruminal turnover of fluids, which may be helpful under HS because the passage rate is slower (Shalit et al., 1991). In a temperate area, high-producing dairy cattle have a water turnover of 135 kg/day during peak milk production, with an average of 99 kg/day (Silanikove, 1989). Lactating dairy cows' total body water is estimated to be between 75 and 81% of their body weight. Water may be lost through the integument and the respiratory system, and these losses rise as the temperature increases (Kibler and Brody, 1952 a).

Behavior

Animals' behavior changes in reaction to high temperatures to lessen the heat burden on the body. Adaptations that reduce heat generation include changing feeding patterns (eating during the colder part of the day) and requiring shade (Bernabucci et al., 2009). These behavioral adaptations help to maintain homeostasis by contributing to thermoregulatory mechanisms. Also, the HS's visible and invisible impacts were shown on the dairy cattle level, as presented in Figure 6.

Behavioral responses to HS

In addition to physiological responses, changes in behavior, such as increased standing time, decreased feed intake, seeking shade, and increased water intake, are other means of thermoregulation (Polsky and von Keyserlingk, 2017). Observing behavioral changes in HS is valuable because the behavior will change before drops in productivity occur (Schütz et al., 2010). During HS, the standing duration rises because this behavior exposes more surfaces to heat loss mechanisms such as sensible water loss, radiating surface area, and air movement via convection (Cook et al., 2007; Allen et al., 2015). Reduced dietary intake lowers the heat generated from digestion and absorption of nutrients (Stull et al., 2008) and lowers metabolism and maintenance energy requirements (Blackshaw and Blackshaw, 1994). Dairy cows kept on grassland will readily accept shade if it is supplied (Kendall et al., 2006), especially when it blocks a greater percentage of solar radiation (Tucker et al., 2008; Schütz et al., 2009), as shade reduces the heat load gained from solar radiation (West, 2003).

Increased water ingestion raises heat loss, and combats dehydration (Vizzotto et al., 2015), as evaporation, is the primary method of heat loss for dairy cows (Collier et al., 1982). Water has a high heat of vaporization and heat capacity, allowing an animal to dissipate and withstand a great amount of heat relative to volume loss and body temperature increase (Murphy, 1992). Water cools the reticulum (Bewley et al., 2008; Ammer et al., 2016), and drinking cooler water can decrease rectal temperature (Wilks et al., 1990).

Standing and lying behavior

Cook et al. (2007) identified a THI threshold of 68 when standing and lying, and behavior begins to change. As THI increases, time spent standing increases from 2.6 h to 4.5 h/d (Cook et al., 2007), and time spent lying decreases from 10.9 h/d to 7.9 h/d (Cook et al., 2007) or from 9.5 h/d to 6.2 h/d (Nordlund et al., 2019). Lying about duration also decreases from 50 min/bout to 33 min/bout as THI increases (Nordlund et al., 2019) and can decrease as much as 30 min/bout (Allen et al., 2015). As core body temperature (CBT) increases from 37.8°C to above 40.5°C, standing duration rises to more than 60 min (Allen et al., 2015).

Allen et al. (2015) and Nordlund et al. (2019) measured the thermodynamics for postural changes. CBT drops on average at 0.25°C/h when standing and increases to 0.50°C/h when lying (Nordlund et al., 2019). The average CBT is 0.2°C lower at the end of standing and 0.17°C higher at the end of lying (Allen et al., 2015). Nordlund et al. (2019) tried to determine the CBT threshold when dairy cows would end up lying bout; however, the CBT range in which cows ended up lying about (39.0–39.6°C) overlapped the CBT range in which they chose to lie down (38.6–39.2°C). Cows quite consistently ended their lying bouts after a net gain in CBT of 0.40–0.48°C; thus, the authors concluded that the net increase in CBT during lying might be a more accurate determinant of when a cow chooses to end lying, as opposed to a specific CBT threshold.

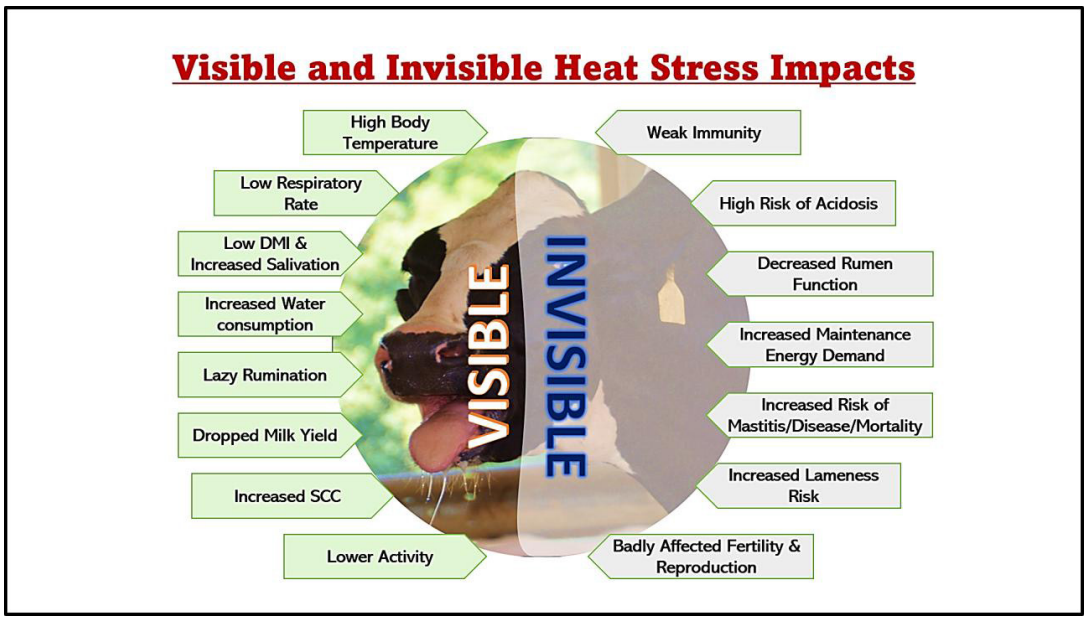


Figure 6. Visible and invisible impacts of the heat stress on the dairy industry

For dairy cows, lying is a high-priority behavior (Munksgaard et al., 2005) that is compromised by HS; in normal conditions, dairy cows choose to lie for between 11.2 h/d (Ito et al., 2010) to nearly 13 h/d (Munksgaard et al., 2005; Fregonesi et al., 2007; Ledgerwood et al., 2010). Increased standing time increases the risk of lameness in dairy cattle (Cook and Nordlund, 2009), a malady frequently associated with an abnormal, likely painful gait (Whay et al., 1997). Thus, heat-stressed dairy cattle with prolonged standing periods may be more susceptible to lameness. Indeed, Cook et al. (2007) reported an elevated prevalence of lame cows at the end of their summer trial. Moreover, severely lame cows spend more time reclining than non-lame cows (Ito et al., 2010); as a result, lame cows may be less able to deal with HS (Cook et al., 2007).

Feeding behavior

For every unit increase in THI between 53 and 76, there was a decreased feed intake by 0.11 kg/d (Ammer et al., 2018), as well as 0.51 kg/d decrease for every unit increase in THI between 72 and 84 (West et al., 2003). Climate-controlled trials where dairy cows were subjected to a short period of HS after thermoneutral conditions have found different results for the magnitude of feed intake decline. Exposure to experimental HS conditions for 4 d resulted in 14.6 kg less feed (Spiers et al., 2004), and for 7 d consumed 6.1 kg less feed (Wheelock et al., 2010) on the last experimental day. Ominski et al. (2002) noted a smaller decline in feed intake of only an average of 1.4 kg/d less over the 5 d of an experimental HS period. These climate-controlled trials differed in how the experimental HS conditions were imposed. During the HS periods, Spiers et al. (2004) maintained the THI at a constant 78, while the other studies used a cyclic THI (ambient temperature range of 20–32°C, Ominski et al., 2002; THI range of 72–82, Wheelock et al., 2010).

Cyclic THI allows for thermal recovery (i.e., reestablishment of normal body temperature) after periods of high temperature through improved heat dissipation when the temperature is lower (Igono et al., 1992). If the night-time ambient temperature is below 21°C for 3–6 h, milk production declines due to elevated THI during the day, which may be mitigated (Igono et al., 1992). The decline in dry matter intake in the Ominski et al. (2002) study may have resulted from the 13 h duration of >21°C ambient night-time temperature. In contrast, feed intake declined, as reported in the Spiers et al. (2004) study, which may be returned to the severe HS impacts given the continuous high THI. Other observed changes in feeding behavior because where feed sorting was considered a consequence of HS (Miller-Cushion et al., 2019) as well as lowered rumination time (Soriani et al., 2013; Moretti et al., 2017). Usually, dairy cows sort in favor of smaller particles (e.g., grain). Still, dairy cows favor longer forage particles in conditions with high THI, possibly due to decreases in rumen pH and possible rumen acidosis (Miller-Cushon et al., 2019).

Rumen pH is also affected by the time spent as increased saliva flow reduces acidosis (Owens et al., 1998). Soriani et al. (2013) found that the rumination period lowered by 2.2 min for every unit rise in daily maximum THI (76), possibly compounding the issue of decreased rumen pH during HS. Reduced feed intake can put cows into a negative energy balance and make them more susceptible to disease (Contreras et al., 2016). Besides the negative health consequences of reduced feed intake for a dairy cow, there is also decreased feed intake, which leads to reduced milk yield (Brown et al., 1977).

Seeking shade

On average, dairy cows use shade for 1.8/6 daylight hours, which increases on days with higher solar radiation (Schütz et al., 2009). Dairy cows will use a shade structure that blocks 25% solar radiation for 1.3/15.5 day-light h and a shade structure that blocks 99% solar radiation for 3.3/15.5 daylight h (Tucker et al., 2008). When offered a choice between shade that blocks 25% or 99% of solar radiation, cattle will spend more time (72.3%) under the 99% shade (Schütz et al., 2009). The extent of the provided shade also affects usage; when offered 9.6 m^2 of shade/cow, cows spend 2.9/5.8-daylight h in the shade, but this value decreased to 1.4 h when there was only 2.4 m^2 of shade/cow (Schütz et al., 2010). Even when dairy cows are reluctant to lie for 12 hours, they will take longer standing in the shade than lying in a non-shaded area with elevated ambient air temperature (Schütz et al., 2008).

When offered two shade structures, not all groups of cows accessed the shade simultaneously, possibly due to increased competition (Kendall et al., 2006). Measuring shade use when competition and space are not limiting factors would be interesting. In contrast, Kendall et al. (2007) recorded a 0.3°C decline in body temperature after cows were given shade during a 90-minute treatment period. The microclimate under the shade that blocked 93% solar radiation was 1°C cooler. Unfortunately, Kendall et al. (2007) failed to clarify whether 1°C refers to ambient or black globe temperature given that shade has little to no effect on ambient temperature (West, 2003) and that they measured heat load index, the authors are likely referring to a 1°C cooler black globe temperature. Similarly, when shade prevents 25%, 55%, and 99% of solar radiation, the corresponding black globe temperature in the shade was 1, 2, and 3°C cooler, respectively (Schütz et al., 2009).

Kendall et al. (2006) speculate that the lack of any change in body temperature resulted from the mild ambient conditions during their study period (average mean ambient temperature = 18.5°C). Although the average ambient temperature conditions in the studies mentioned above were similar (19.5°C, Kendall et al., 2007; 16°C, Schütz et al., 2009; 18°C, Schütz et al., 2010; 20.7°C, Palacio et al., 2015). Palacio et al. (2015) speculated that the failure to note any differences in body temperature between shaded and non-shaded cows may be due to the

use of cows to alternative strategies for cooling, such as elevated time passed around the water trough, where the area around a water trough may have a cooler microclimate (Palacio et al., 2015). Schütz et al. (2010) show that a preferred location to stand for non-shaded cows can decrease body temperature. Some studies reported that shade reduced the body temperature and temperature underneath the shade structure (Schütz et al., 2009), while others did not report this (Schütz et al., 2010; Palacio et al., 2015). For example, the shade structure provided by Kendall et al. (2007) blocked solar radiation from above and on three sides, whereas the other studies only blocked solar radiation from above. Offering a more expansive shade structure may allow the cows to reduce their body temperature more effectively by minimizing heat from solar radiation. Indeed, Hahn et al. (1963) found that placing shade on top of an animal reduced radiant heat gain from the sun by 45%, but this increased to 54% when the other three walls were shaded. Schütz et al. (2009) provided the largest space allowance per cow (16 m^2/cow for three cows) compared to the other studies such as 1.8 m^2/cow for ten cows (Kendall et al., 2006), 1.25 m^2/cow for four cows (Kendall et al., 2007), 2.4 and 9.6 m^2/cow for ten cows (Schütz et al., 2010) and 4.65 m^2/cow for four cows (Palacio et al., 2015).

The quantity of radiative heat transmission between two bodies reduces as their distance increases (Polder and Van Hove, 1971); the increased space allowance per cow provided underneath the shade structure by Schütz et al. (2009) may have resulted in less radiating heat, thus lowering the ambient temperature in the shaded area. However, there are numerous anecdotal accounts that dairy cows bunched together when heat stressed (Drovers, 2015; Farming Independent, 2018), a behavior that increases the radiative heat transfer between animals. However, little is known about the motivation for this behavior. The grouping may be a protective response to stress (Mooring and Hart, 1992) or perhaps a desire of all to be in a preferred environment. An alternative form of shade provision that reduces rectal temperature is offering access to cows to the shade provided by two elm trees and one artificial shade structure that collectively blocked 80% of solar radiation (Valtorta et al., 1997). These authors found that shaded cows had a lower rectal temperature (39.3°C) than non-shaded cows (40.1°C). Trees may be better than artificial shelters because leaf evaporation offers additional cooling (Van laer et al., 2015). Veissier et al. (2018) also investigated shade given by trees with shade cloth strung between them and found that shaded cows tended to have a lower rectal temperature than non-shaded cows. Lastly, Kendall et al. (2006) and Schütz et al. (2010) commented on the challenges of providing shade to a group of cows where competition may prevent an individual cow from accessing the shade resource. As a result, studies that reported no impact of shade on cow body temperature may not be a fair depiction of shade's efficiency.

Drinking behavior

Multiple studies have found that drinking increases during elevated ambient temperature and THI (Murphy et al., 1983; Meyer et al., 2004; Beatty et al., 2006; Cook et al., 2007; Cardot et al., 2008; Ammer et al., 2018). As THI increases from 56 to 78, drinking time can double, from 0.26 h/d to 0.5 h/d (Cook et al., 2007). In an average THI range between 53 and 76, water intake increases by 0.96–1.08 L/d, and drinking frequency increases by 0.12–0.23 bouts/d per rising THI unit (Ammer et al., 2018).

Water intake increases by 0.84 L/d per °C in average ambient temperature and by 1.89 L/d per °C in maximum ambient temperature (Meyer et al., 2004). Regarding minimum ambient temperature, water consumption increases by 1.2 L/d per °C (Meyer et al., 2004). Drinking of water can also increase when alternative forms of cooling are limited. As heat load increases, unshaded cows spend more period at the water trough than shaded cows (0.7/5.8 h for unshaded cows versus 0.1–0.3/5.8 h for shaded cows) (Schütz et al., 2010), (0.8/3 h for unshaded cows versus 0.1/3 h for shaded cows) (Palacio et al., 2015). Unfortunately, these studies did not include other measures of drinking behavior, such as water intake. Changes in drinking behavior are less commonly employed as non-productivity-related markers of HS in dairy cows than eating and resting behavior (Galán et al., 2018). However, the significant increases in water intake, drinking time, and frequency of drinking in response to HS suggest that drinking behavior is a helpful predictor of heat load in lactating cows and warrants additional investigation, as shown in Figure 7.

Competition for cooling resources

Shade and water are valuable cooling resources for a heat-stressed dairy cow (Dash et al., 2016), and the cattle become more aggressive when warm (Coimbra et al., 2012). When less shade is available per cow, dairy cows engage in aggressive interactions to gain access to shade (Schütz et al., 2010; Stivanin et al., 2019). Dairy cows engage in an average of 0.2 competitive interactions/h when there is 10 m^2 of shade per cow, but this increases to 0.5 competitive interactions/h when there is only 2 m^2 of shade per cow (Stivanin et al., 2019).

In a group of 10 cows during a 5.8 h observation period, Schütz et al. (2010) found the total number of aggressive interactions per m^2 of shade increased from 3.2 when there was 9.6 m^2 of shade per cow to 10.7 when there was 2.4 m^2 of shade per cow. Competition near the water trough also increases when shade is not provided (Vizzotto et al., 2015) or in small amounts (Stivanin et al., 2019). While shaded cows will engage in an average of 0.12 competitive events per day to gain proximity to the water trough, this number increases to 0.35 for unshaded cows (Vizzotto et al., 2015). When the amount of shade per cow decreases from 10 to 2 m^2, the average number of competitive events per cow near the water trough increases from 0.2/h to 0.8/h (Stivanin et al., 2019). Thus, research is required on competition at the drinker for free stall-housed dairy cows.

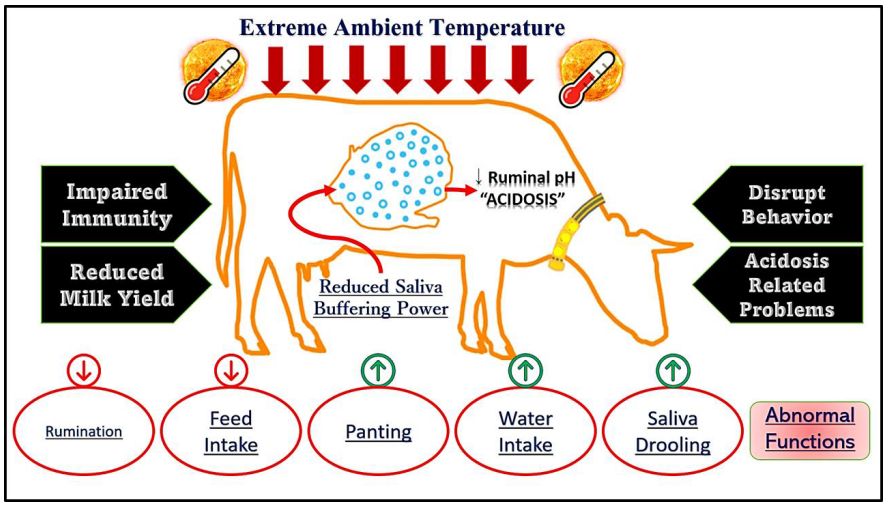


Figure 7. How heat stress clinically affects dairy cows with associated disease problems

Production impact

HS has a detrimental impact on milk yield and feed consumption and can have long-term consequences on milk production. Milk output falls as THI rises, and milk composition changes, with less fat and protein generated (Ravagnolo et al., 2000; Hammami et al., 2013; Bernabucci et al., 2014). Milk yield could be decreased by 0.2 kg/d per unit increase in THI over 72 (Ravagnolo et al., 2000), 0.41 kg/d per unit increase in THI over 69 (Bouraoui et al., 2002), 0.88 kg/d per unit increase in THI measured two days earlier (West et al., 2003), and up to 0.96 kg/d per unit increase in THI between 70 and 74 (Hammami et al., 2013). According to Johnson (1987), the slope of milk output loss during HS is steeper (0.059%/cow/day) in higher-producing (30 kg/day) cows than in lower-producing (25 kg/day) cows (0.019%/cow/day). The decrease in milk output and consumed feed shows a temporal lag from initial heat exposure.

Milk output is reduced 24 to 48 hours after being exposed to THI levels of more than 80 (Collier et al., 1981). Furthermore, discrepancies between estimates of decreased milk yield in response to increased THI or estimates for any responses to HS may partly be explained by the different conditions under which studies were conducted. For example, some studies have been conducted under the Mediterranean (Bouraoui et al., 2002), subtropical (Ravagnolo et al., 2000), hot, humid (West et al., 2003), and temperate (Hammami et al., 2013) conditions. HS THI thresholds for dairy cows are higher in semiarid climates (ambient temperature 30°C at 25% RH) than in hot, humid climates (ambient temperature 23°C at 75% RH) (Bohmanova et al., 2007). Cows in temperate climates have lower HS thresholds of an ambient temperature of 17.8°C at 75% RH (Hammami et al., 2013).

Cattle can adapt to gradual and prolonged changes in environmental conditions (Collier et al., 2019). The protracted heat loads in subtropical climates allow better acclimation to environmental conditions, e.g., reduced metabolic rate, changes to the cardiovascular system, more efficient heat loss, and changes to morphology (Renaudeau et al., 2012). Cattle in temperate climates cannot acclimate to heat because they are only exposed to acute HS events during the summer (Renaudeau et al., 2012). Thus, the lower THI thresholds of dairy cows in temperate versus subtropical climates could be related to the different heat tolerances of the animals. This may partly explain why Ravagnolo et al. (2000) noticed the smallest decrease in milk yield (0.2 kg/d) in a subtropical climate, and Hammami et al. (2013) found the largest decrease in milk production (0.96 kg/d) in a temperate climate.

Furthermore, when climatic factors were examined on the same day as milk yield and DMI per unit rise in THI, the fall in milk production and DMI per unit increase in THI were much less than when climatic variables were tested two days earlier (West, 2003). This shows that the full effect of a heat event is prolonged, which may be connected to the time lag between ingested food and utilization and energy partitioning. A frequent physical response to high temperature is a decrease in feed intake.

When the ambient temperature is high, the hypothalamus's rostral cooling center stimulates the medial satiety axis while inhibiting the lateral appetite center (Albright and Alliston, 1971). When the ambient temperature climbed from 18 to 30°C, nursing Holstein cows consumed 5% less concentrate and 22% less roughage, resulting in reduced milk output, according to McDowell et al. (1976). Forced feeding experiments revealed that maintaining basal levels of feed intake alleviates the reduction in milk yield caused by increased temperature (Wayman et al., 1962). Furthermore, pair-feeding trials revealed that lower nutritional intake accounts for 35% (Rhoads et al., 2011) and 50% (Wheelock et al., 2010) of the drop in milk output caused by HS. However, lower appetite and nutritional intake can be ascribed to a significant drop in milk supply under HS.

When comparing HS studies on dairy cows, it is important to consider the climate. Studies showed that maintenance of energy requirements increased during HS, so the energy available for milk synthesis is reduced (West, 2003). Also, studies have found HS to increase the frequency of various illnesses in dairy cattle, including metabolic problems and mastitis (Das et al., 2016; Dahl et al., 2020). HS has also been linked to higher mortality in dairy cattle. These health concerns might be caused by the reduced immunological function reported in heat-stressed dairy animals (Bishop-Williams et al., 2015; Gonzalez-Rivas et al., 2020).

Furthermore, Ferreira and De Vries (2015) discovered that bulk tank somatic cell counts (SCC) in milk from hot, humid parts of Florida were greater than in milk from lower temperature locations (Zucali et al., 2011; Smith et al., 2013; Nasr and El-Tarabany, 2017).

According to Bandaranayaka and Holmes (1976), milk's lipid and protein concentrations were reduced considerably at 30°C ambient temperature compared to cows in thermoneutral circumstances. In addition to the negative impact of decreased milk yield, changes in milk composition are detrimental for Canadian dairy farmers because compensation is based on milk composition (e.g., butterfat, protein, and other solids) (Ouellet et al., 2019).

On the clinical level of mastitis in dairy cows, under HS conditions, dairy cattle reacted by altering physical, metabolic, and molecular processes to neutralize HS (Baumgard and Rhoads, 2012; Hu et al., 2016). This, furthermore, would reduce the antioxidant capacity and immunological function of the mammary tissues, resulting in increased intramammary infections (IMI) (Almeida et al., 2018; Zou et al., 2019). HS also causes molecular changes in mammary cells associated with milk component production and mammary cell turnover (Salama et al., 2019) as well and HS inhibits cell development, causing changes in structural proteins, membrane permeability, and metabolism in bovine mammary epithelial cells "bMECs" (Salama et al., 2019). This theory would explain the metric changes in the milk constituents.

Considering the impact of HS on cattle during the dry period, the transition phase from gestation to lactation is critical in the dairy cow production cycle for mammary gland growth, dietary intake, and overall production performance for the subsequent lactation (Thompson and Dahl, 2012; Fabris et al., 2019). On the other hand, dry cows frequently have less management intensity because this is viewed as a non-productive phase (Fabris et al., 2019). Dry cows produce less metabolic heat than nursing cows, which mitigates the negative consequences of high THI (West, 2003; Tao et al., 2011; Ferreira et al., 2016; Skibiel et al., 2018).

Thermal stress has a major impact on the dry period of dairy cows, raising rectal temperature, respiration rate, and plasma prolactin concentration while lowering dry matter intake, body weight increase, gestation duration, and calf birth weight (Amaral et al., 2009, 2011; Tao et al., 2011; Wohlgemuth et al., 2016; Fabris et al., 2017, 2019). In the same way, HS has a harmful influence on lymphocyte proliferation in dairy cows. There is evidence that the length and intensity of HS might damage immunological function (Amaral et al., 2010). Furthermore, it was found that hepatic metabolic gene expression was downregulated in heat-stressed dry cows at the lactation beginning, with increased oxidative burst and phagocytosis in cooled cows (Amaral et al., 2011). They also assessed the immunological state by measuring immunoglobulin G released in response to the ovalbumin challenge. They hypothesized that reducing HS during the dry season increased production output and immunity in the subsequent lactation (Amaral et al., 2011). Parallelly, Thompson and Dahl (2012) investigated the effects of dry period season on subsequent lactation regarding production performance, the occurrence of health disorders, and reproduction performance by including more than 2600 calving records over three consecutive years on a commercial dairy farm in Florida and reported that cows dried off in hot months had a higher occurrence of postpartum disease like mastitis, respiratory problems, and retained fetal membranes in early lactation compared with cows dried during cool months.

Several recent studies have also examined how heat exposure during the dry season affects udder growth and mastitis management. HS reduced the rate of udder cell multiplication but did not affect udder cell death (Tao et al., 2011). Wohlgemuth et al. (2016) expanded these findings to indicate changes in autophagic activity early in the dry phase. Since autophagy appears essential for the optimum future proliferation of mammary cells, this may explain some of the harmful consequences of HS. Skibiel et al. (2018) used a comprehensive bovine liver proteomics investigation of postpartum cattle to identify differentially expressed proteins and examine protein modifications caused by HS during the dry period. The most relevant pathways affected by dry-period HS were hepatic oxidative phosphorylation and mitochondrial dysfunction; however, dry-period cooling helped to increase ATP production while reducing oxidative stress, inhibited the excessive accumulation of hepatic lipids in the liver that may be reliable for fatty liver, and provided sufficient metabolic support for higher milk production in the subsequent lactation. As a result, HS management measures may be required during the dry season to promote optimum lactation and reduce vulnerability to transitional disorders.

Reproduction and fertility

Thermal stress has a well-documented impact on reproduction in dairy animals. Higher core body temperature adversely influences conception rate, elevates early embryonic mortalities, decreases the period and intensity of estrus expression, raises the days' sum to uterine involution, and decreases postpartum maximum progesterone levels (Fuquay, 1981; Hanafi et al., 2023), as presented in Figure 8. Heat load compromises reproduction problems,

including reduced pregnancy success rates and embryonic survival (Hansen, 2007). Around breeding, plasma hormone concentrations undergo a dynamic change that can be negatively affected by HS (Ingraham et al., 1974). Ovulation failure is 9% higher, and the pregnancy rate is 16% lower for cows inseminated in the warm season compared to the cold season (López-Gatius et al., 2005). Conception rates can decline as much as 45% when the average THI on the second day before breeding increases from 70 to 84 (Ingraham et al., 1974). The differences between these studies may be due to differing levels of ambient conditions the cows were exposed to, where López-Gatius et al. (2005) only measured the impacts of the season (the warm period was when an average of 20–31 days in a month had a maximum temperature above 25°C), while Ingraham et al. (1974) directly accounted for THI (a THI of 84 equated to above 30°C).

Estrus is the external sign of ovulation, and identifying estrus is imperative for the correct timing of insemination for pregnancy success (Roelofs et al., 2010). HS can make estrus behavior harder to detect due to the shortened duration and intensity of visible signs, and this might explain the reduced pregnancy rates during HS (De Rensis et al., 2015). Dairy cattle in the summer have a 0.7 h shorter duration of estrus and take 144 fewer steps/h on the day of estrus than cows in the winter (Sakatani et al., 2012). The pregnancy loss doubled for every unit increase in the cumulative number of hours with a THI >85 during days 11–20 of gestation (Santolaria et al., 2010). During days 21–30 of gestation, the likelihood of pregnancy loss increases by a factor of 1 for every unit rise in mean maximum THI (García-Ispierto et al., 2006). Finally, HS makes it difficult for dairy cows to sustain milk output, become pregnant, and remain pregnant. Involuntary culling choices on dairy farms are made for various reasons, including low milk production and reproduction (Hadley et al., 2006; Bell et al., 2010).

Adaptation to HS

HS adaptation is a homeostatic mechanism mediated by the endocrine system. Acute and chronic acclimatization to temperature stress requires alterations in the production of hormones and receptors in particular cells. Both stages take weeks rather than days to achieve heat adaptation (Collier et al., 2006 a). There is proof for a biphasic sequence of thermal acclimatization, classified as short-term or long-term. Short-term thermal acclimatization begins at the cellular level, causing alterations in cellular signaling and pathways that disrupt cellular homeostasis and reprogram cells to continue (Horowitz, 2001).

Before adaptation, the immediate reactions to heat in ruminants involve elevated thermal dissipation, predominantly through evaporative heat loss mechanisms, lowered feed consumption, and elevated drinking (Horowitz, 2001, 2002). Long-term thermal adaptation occurs after the first short-term adaptation has been completed and is characterized by changes in gene expression that HSP predominantly mediates (Horowitz, 2002; Zhang et al., 2023). Endocrine modifications are established during this period to sustain the procured homeostasis. Adapted reactions are caused by a hormonal connection in the pathway from the CNS to peripherals, and they generally change the response of effector cells or organs to an ecological stimulus. This directs metabolism to reach a new evenness, which may be considered a new physiological status (Bernabucci et al., 2010).

Acclimatization involves endocrine alterations such as decreased concentrations of thyroxine (T4) and triiodothyronine (T3), which reduces the basal metabolic level (Johnson, 1987; Nikanorova et al., 2023; Zwahlen et al., 2024). Glucocorticoid, growth hormone, and catecholamine levels are all lowered after extended heat load exposure (Yousef, 1985; Hannan et al., 2024; Idris et al., 2024).

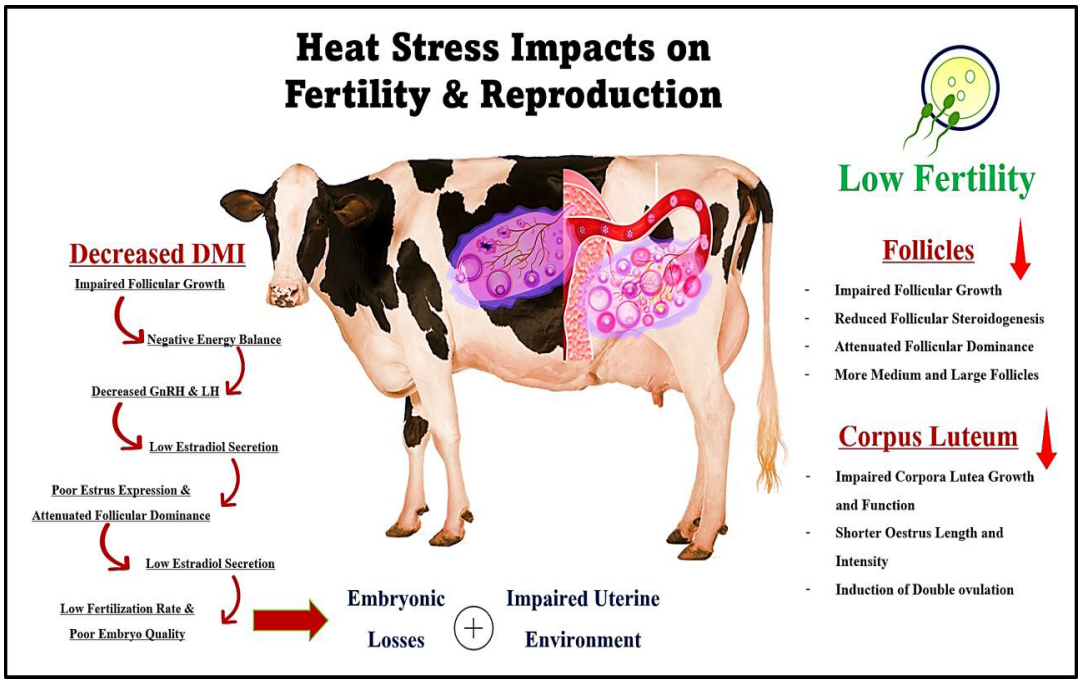


Figure 8. Reproductive and fertility problems associated with heat stress and cascaded mechanism of embryonic losses and impaired uterine ecology

Phenotypic adaptation refers to physiological or behavioral changes over an animal's lifetime that reduce stress or enhance the capability to overcome stressors (Bernabucci et al., 2010).

The physiological response in a cow that reduces the events caused by environmental alterations is called adaptation (Glossary of terms for thermal physiology, 1987; Dos Santos et al., 2021). This alteration might be phenotypic and occur throughout the cow's life, or it could be genetic and result from selection within the species. Adaptation thus indicates the phenotypic alterations to certain ecological conditions. The term accommodation means the animal's overall ecosystem to which it changes. Acclimatization to HS can also be affected by pre-stress milk yield, as lowered-yielding dairy can return to pre-stress levels sooner. In contrast, high-yielding cattle require longer recovery and may not return to pre-stress stages for the rest of the lactation period (Johnson and Vanjonack, 1976; Liu et al., 2023). This is when milk output, feed intake, and metabolic heat generation rise, and the zone of thermo-neutrality shifts to lower temperatures (Kadzere et al., 2002).

Genetics and thermal tolerance

Genetic factors impact how an individual responds to HS, and there is a great deal of diversity among animals and breeds within species (Gaughan et al., 2009; Robinson et al., 2023). The obvious trade-off between high output and a herd capacity to keep homeostasis when faced with metabolic and HS concerns breeders of high-producing cattle. Genetic selection has diminished heat tolerance for improved milk output (Gaughan et al., 2009). Negative relationships have been shown between thermal tolerance characteristics (sweating response) and milk yield and metabolic level, demonstrating the difficulty of breeding for thermal tolerance while preserving productivity (Finch et al., 2009). Thermal tolerance is one of cattle's most significant adaptation features. Identifying heat-tolerant cows within high yielders will be advantageous if these cows can also maintain output during difficult heat situations (Gaughan et al., 2009). The heritability of anatomical and morphological features like sweat gland density and action, hair coat color, density, length, and thickness has been studied in numerous ruminant breeds (Nardone, 1998; do Nascimento Barreto et al., 2024).

Disparities in anatomy and physical traits describe variations in thermal tolerance among species and breeds (Collier et al., 2008; Freitas et al., 2021). The capacity to sustain rectal temperature is a well-accepted parameter of thermal tolerance (Yousef, 1985; Mohammed et al., 2023). However, its heritability is poorly documented; only a report showed its decrease (0.16–0.64) (Nardone et al., 1998). A quantifiable heat tolerance characteristic, such as rectal temperature or milk yield, must be identified to pick out and designate cows as thermal tolerant among the breeds. West (2003) and Bernabucci et al. (2010) proposed that heat tolerance may be selected while sustaining productivity. Nguyen et al. (2016) established genomic selection for thermal tolerance in Australian dairy relies on the capacity to retain milk supply during HS. However, genetic selection has yet to be confirmed in a referred population.

The amount of output lost from HS varies between animals and is believed to be genetically determined. Genetic characteristics heavily impact the threshold of climatic circumstances that cause output drops. When the temperature humidity index (THI) reaches the thermoneutral threshold of cow comfort, the genetic variation for thermal tolerance rises (Ravagnolo et al., 2000; Cheruiyot et al., 2022). It may not be economical to undertake management methods to mitigate the destructive impacts on output. As a result, breeding dairy cattle for thermal tolerance may be the most potent way to alleviate HS. As the occurrence of heat waves in dairying regions increases, the pace of genetic gain for heat tolerance must be expedited (BoM, 2014).

Handling the genomic selection arm to identify dairy animals that are genetically more thermal tolerant is an imperative tactic for HS moderation; when combined with other managing procedures, such as more targeted nutrition during HS, it can result in marked paybacks for the dairy business in the hot season.

HS and gene expression

There is little evidence documenting cow's gene expression alterations *in vivo* in response to HS, with no data accessible for the *Bos taurus* dairy cattle breeds. The introduction of high-throughput genome sequencing has opened the possibility of complete transcriptome analysis. Mehla et al. (2014) studied the global gene expression alterations in the peripheral blood of *Bos indicus* (zebu) cattle subjected to 42°C and 95% RH for 4 h. The researchers discovered that brief contact with extreme HS changes the expression of genes in fat and carbohydrate metabolism and immune response, with upregulation of genes in protein breakdown, transport, and downregulation of protein formation.

A class of heat shock proteins is upregulated under HS. HSPs are molecular chaperones categorized based on their level or action. They are HSP100, HSP90, HSP70, HSP60, and HSP40, with HSP with molecular weights 70 and 90 being the most pronouncedly expressed under HS (Guerriero and Raynes, 1990; Bernabucci et al., 2010; Richter et al., 2010; Collier et al., 2019). Protein production is supported by molecular chaperones, which aid in folding nascent polypeptides. These molecular chaperones inhibit aggregation by avoiding non-specific reactions and aid in the translocation of proteins to their proper intracellular site. When a protein is broken, molecular chaperones aid in refolding or elimination through cell disintegration (Powers and Workman, 2007).

The beginning of HSP gene expression in a stress reaction is part of a well-organized sequence of biochemical and genetic processes that define the heat shock response (HSR) (Powers and Workman, 2007). The be-

ginning of this interaction promotes cytoprotection from a stressor that might cause deadly molecular destruction (Westerheide and Morimoto, 2005).

The heat shock factor (HSF) transcription family has been proposed as a crucial initial responder throughout the beginning of increased cell temperature. These transcription factors have a role in coordinating cellular responses, like the suppression of apoptosis. Page et al. (2006) characterized the HSF1 signaling network below unstressed and stressed situations. They discovered that when heated, heat shock proteins (HSP) dissociate from HSF1 monomers, which subsequently unfold and bind to 2 other HSF1 monomers to form trimers before nuclear translocation. They subsequently move to the nucleus, where homotrimeric HSF1 binds promoters, including heat shock elements (HSE), to trigger HS gene expression. HSF1 was linked to the control of glucose metabolism and the ubiquitination reactions to HS (Page et al., 2006). While HSPs are directly associated with HS, additional alterations in the expression of many other genes are not correlated to organism persistence.

The data offered by gene expression assessment makes it accessible to make assumptions regarding specific biological processes implicated in HS reactions. Gene expression assessment of individual cells gives data on the physiological status of the cells. The quantity of cells in a tissue is governed by the rates of cell movement, division, and death (Strasser et al., 2000; Cumming and Levayer, 2024). The amount of programmed cell death (apoptosis) is hypothesized to relate to the decreased milk synthesis (Pollott et al., 2014). Apoptosis is when damaged cells that have reached the end-up of their productive life are eliminated from the body to avoid the harm of stress reaction and assist healing (Beere, 2004; Salama et al., 2023).

Most gene expression studies in the cow udder have used tissue biopsy. Tissue biopsy is an invasive treatment that raises issues about animal welfare (Canovas et al., 2010). Because the udder is highly heterogeneous, tissue obtained by biopsy may not be typical of milk synthesis, tissue, and mammary biology (Brenaut et al., 2012).

Gene expression in somatic milk cells is a viable alternative to udder tissue biopsy. As mRNA may be recovered from somatic cells identified during milking, Medrano et al. (2010) developed an alternate approach for collecting high-quality RNA to research gene expression in the cow udder. The similarities in mRNA gene expression between somatic milk cells and mammary tissue imply that milk could be employed as a viable substitute for gene expression investigations of the cow udder (Medrano et al., 2010). SCC in the cell layer of the skim milk part of whole milk has many immune cells and a low proportion of udder epithelial cells, which carry gene expression data important to udder gland physiology. Repeated specimens might be collected from cows using this approach to provide estimates of temporal gene expression behavior throughout time, which is impossible with tissue biopsy.

Combined with physiological data, this information will help researchers better understand the relationships between physiological status and gene expression in the cow udder. Collier et al. (2006 a) performed an *in vitro* trial to evaluate the impact of temperature stress on cows' udder growth and gene expression in a bovine udder cell collagen gel culture system. The ductal branches were inhibited and regressed due to the acute HS (42°C). Gene expression profiling revealed an overall increase of genes involved in stress response, DNA repair, and protein repair. Downregulated genes during HS were shown to be involved in cellular and udder epithelial cell-specific biosynthesis, cell cycle, structural proteins, metabolism, and morphogenesis (Collier et al., 2006 b). This suggests that the udder ceases cell development and ductal branching during HS and reverts to cell survival mechanisms. HSP70 gene expression increased considerably during 1 and 2 h after HS and peaked within 4 h. Bovine udder epithelial cells lost thermotolerance and returned to baseline HSP70 expression 8 hours after thermal stress.

The cell stress reaction and apoptosis are linked, and it was shown that HSPs modulate the apoptotic pathway and HSP transcription is involved in the destruction and refolding of stress-damaged proteins (Samali and Orrenius, 1998; Fu et al., 2022). Hu et al. (2016) found that udder cell death and defense reaction to 38–42°C *in vitro* in Holstein Friesian were consistent with these findings. The return of HSP70 gene expression to baseline coincided with a rise in genes implicated in apoptosis, suggesting that these proteins were undergoing programmed cell death. There was also a transcriptional decrease in genes included in milk formation, recommending that HS-induced milk output losses are linked to a reduction in the expression of genes governing milk production. During 12 h of HS, apoptosis rates peaked at 3 and 5 h, while HSP70 transcription quickly increased to 0.5, 1, and 3 h.

Conclusions

Climate change is becoming a global problem, with significant consequences for dairy cow performance and welfare. Thermal stress is a physiological status that harms multiple physiological systems in dairy cattle, involving general health, immunity, reproduction, and productivity throughout their life cycle. It is characterized by a progressive rise in global temperature with the risk of extreme weather events. HS also directly affects newborn calves' passive and cellular immunity, which may describe why calves die more in the summer. Similarly, growing heifers perform worse in hot environments. However, the impacts of hyperthermia on heifer immune action are inconclusive. Finally, this comprehensive research provides hands-on experience with HS's distinct components versus the normal physiologic process of adapting and acclimatizing dairy cattle to HS. More research is required to develop potent and low-cost cooling methods for dairy cattle, pre-weaned calves, and growing heifers to maintain immunity alongside good field performance and welfare.

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