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Comprehensive review of heat stress effects on dairy cattle: the implications for production, reproduction, and adaptation in the context of climate change

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ABSTRACT

Heat stress poses a significant threat to dairy cattle, impacting their physiological, reproductive, and production performance. This review aims to provide an in-depth examination of the effects of heat stress on dairy cattle, focusing on how elevated ambient temperatures influence milk production, reproductive efficiency, and overall animal health. The physiological responses to heat stress, including increased respiration rate, elevated body temperature, and changes in feeding and drinking behaviors were analysed and discussed. Heat stress leads to a decrease in feed intake, an increase in water consumption, reduced growth rates, and diminished milk yield and quality. Reproductive performance is also adversely affected, with reduced fertility and increased risk of embryonic loss. Dairy breeds, particularly those with higher production levels, are more susceptible to heat stress due to their higher metabolic heat production. The review highlights the impact of heat stress on the immune and endocrine systems, increasing vulnerability to diseases and inflammatory conditions. Given the limited capacity of animals to adapt to the rapid pace of climate change, the review underscores the need for effective management strategies, including environmental modifications and genetic selection, to mitigate the adverse effects of heat stress. Finally, sustainable dairy farming remains a significant challenge in the context of global climate change and rising temperatures.

Key words: heat stress; dairy cattle; physiological responses; production performance; animal behavior

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Introduction

Climate change exerts uneven impacts on agricultural production, depending on local geographical characteristics (CISCAR et al., 2018). Livestock systems themselves can drive certain climate changes through the emission of greenhouse gases, such as CO_2, N_2O, NH_4, and CH_4 originating from enteric fermentation, manure, slurry, and other sources (THORNTON et al., 2011). In Europe, livestock production systems account for about one-third (approximately 28%) of agricultural land, with a relatively stable livestock population (LEIP et al., 2015). Climate change and microclimatic conditions primarily exert indirect effects on livestock through various impacts on the quantity and quality of feed and water, the presence of pathogens, disease outbreaks, and dis- ease vectors, while direct impacts can have more severe consequences. Extreme temperatures can occur on different temporal (daily, monthly, sea- sonal, annual, decadal) and spatial scales (local, regional, global), and prolonged extreme heat can result in "heat waves" (VICENTE-SERRANO et al., 2015). Healthy and productive animals are the cornerstone of successful livestock production, as farmers aim to avoid reliance on continuous use of supplementary interventions to prevent production problems and treat diseases (SVENSSON et al., 2018). Health issues contribute to financial losses in production, and managing the health of animals and the overall herd is a daily responsibility (ATKINSON, 2019). Furthermore, climate change and microclimatic conditions can impact animals by altering environmental parameters, such as air temperature, relative humidity, precipitation patterns, and the frequency and intensity of extreme events (heat waves, storms, droughts, floods) (SEJIAN et al., 2012). The factors leading to the impact of climate change on animal health are complex and interrelated, acting in a combined and cumulative manner rather than in isolation. Heat stress triggers physiological and behavioral responses in animals, influenced by the animals' genetic makeup and environmental factors, all coordinated by the endocrine, cardiorespiratory, and immune systems (ST-PIERRE et al., 2003). The sensitivity of dairy cattle to heat stress increases with higher milk production, as the generation of metabolic energy rises with the level of milk production. Therefore, it is necessary to mitigate the adverse effects of climate change through the development of management strategies and genetic selection of animals that are more resilient to heat (NARDONE et al., 2010).

Given that heat stress is a prevalent and financially burdensome issue in the dairy cattle industry, the goal of this review was to undertake a thorough assessment of the ramifications of climatic and microclimatic conditions on the welfare, productivity, and reproductive efficiency of cattle.

Indirect effects of climate and microclimatic conditions on cattle

The indirect effects of climate and microclimatic conditions on farms tend to be more long-term and complex compared to the direct impacts. These effects encompass the influence of climate on microbial density and distribution, the distribution of disease-carrying vectors, food and water scarcity, and foodborne diseases (LACETERA, 2018). Consequently, these indirect effects significantly impact the biology and distribution of various vectors.

The impact of climate and microclimatic conditions on disease vectors. Changes in temperature, precipitation patterns, humidity, and wind in temperate climates positively affect insect reproduction and density. An increase in average temperatures has been associated with a higher incidence of mastitis in dairy cattle breeds ($P<0.01$), while dairy buffaloes are less affected (JINGAR et al., 2017). The increased frequency of mastitis in lactating cows may be attributed to high temperature-humidity conditions that facilitate the survival and multiplication of flies, which act as vectors for udder infections. A simulation model tested by WITTMANN et al. (2001), which incorporated a 2°C increase in temperature, indicated the potential for the extensive spread of the insect *Culicoides imicola*, the primary vector of the bluetongue virus, a disease that primarily affects domestic and wild ruminants. Another example of how climate change can indirectly influence animal health is the emergence of parasitic diseases. Gastrointestinal nematodes are parasites with significant portions of their life cycles completed outside the host, making their development highly susceptible to climate change. Research simulations by ROSE et al. (2015) predicted that climate change could affect the annual infection pressure, depending on the species of parasites involved. DHAKAL et al. (2023) report the increased prevalence of external parasites and flies as a primary concern in warmer and temperate climates.

Cattle body hygiene reflects the environmental conditions in which they are kept, and influences aspects of their health under unfavorable microclimatic conditions. The skin and hair serve as a body cover composed of various layers (epidermis, dermis, subcutis), along with their products (hair, keratinous structures), and associated glands (sweat, sebaceous). The skin, being the largest organ in the body, plays multiple roles (protective, thermoregulatory, sensory, excretory, absorptive, etc.). Skin changes can result from various causes, including housing conditions, environment, and management practices (KIELLAND et al., 2009). In the context of cattle welfare assessment, changes in the skin and hooves can also result from inadequate nutrition, predisposing animals to lesions (SCHULZE et al., 2009). Providing adequate space for movement, meeting basic life needs, and facilitating communication with other animals in the same environment lead to better productivity in farm animals. Consequently, the relationship between animals and humans, as well as their mutual interactions, impact both the health and the productivity of farm animals (HEMSWORTH and COLEMAN, 2011). Research indicates that cows exhibit aversion to dirty environments and tend to avoid them whenever possible (PHILLIPS and MORRIS, 2002). Udder and distal limb hygiene are particularly important due to the risk of microorganisms infecting the udder (SCHREINER and RUEGG, 2003). According to COOK (2007), an unacceptable level of dirtiness in three body regions of cows is used as an indicator for assessing cow welfare and health. The study by OSTOJIĆ-ANDRIĆ et al. (2011) found that the housing system significantly influenced ($P \leq 0.05$) the incidence of hair loss, lesions, and swelling. The proportion of cows with lesions/swelling in a free housing system was 6.81%, while it was double, 13.68%, in a tied housing system. Research by VUČEMILO et al. (2012) noted that the housing system significantly affected ($P < 0.01$) the body condition of cows, with a significantly higher proportion of cows in poor condition observed in the free housing system compared to the tied system.

Impact of climate and microclimatic conditions on mycotoxicosis incidence. Another mechanism through which climate change negatively impacts the health of both animals and humans is the promotion of fungal growth and mycotoxin production under high temperature and humidity conditions. The growth of fungi and their toxin production are closely linked to environmental temperature and moisture levels, which depend on weather conditions during harvest, drying techniques, and grain storage (KRNJAJA et al., 2015; KRNJAJA et al., 2018; KRNJAJA et al., 2019). Mycotoxins can lead to episodes of acute illness when animals consume critical amounts of contaminated feed. Aflatoxin B1 (AFB1) is a primary hepatotoxin, while deoxynivalenol (DON) causes digestive disorders, vomiting, anemia, hemorrhage, immunosuppression, and neurotoxic effects. Fumonisins (FB123) are associated with leukoencephalomalacia and pulmonary edema (BERARDO et al., 2011). Mycotoxins can negatively affect specific tissues and organs, including the liver, kidneys, oral and gastric mucosa, brain, or reproductive tract. Some mycotoxins can interfere with natural disease resistance mechanisms and weaken immune responses (STREIT et al., 2012). Measures to reduce mycotoxin concentrations in cattle feed include the use of natural adsorbents based on clays (MIĆIĆ et al., 2017). However, mycotoxin concentrations in feed are often below the levels that would cause acute illness.

Direct impacts of climate and microclimatic conditions on cattle

The immediate direct impacts of climate change on animal health primarily occur due to increased temperature, and the frequency and intensity of heat waves (GAUGHAN et al., 2009). These effects are indicative of heat stress conditions, which, depending on their intensity and duration, can adversely affect animal health by causing metabolic alterations, oxidative stress, immunosuppression, decreased production and overall health, and ultimately, the death of the animal. Animals respond to stress first through behavioral changes, followed by physiological responses, or a combination of both. The animal's reaction to stress varies on the basis of its prior experience of stressors, the intensity and duration of these stressors, the physiological status of the animal, and other factors (MAURYA et al., 2015).

Metabolic disorders. Metabolic stress represents an imbalance between nutrient intake and distribution, where the genetic makeup of dairy cows is pushed towards maximizing nutrient conversion into milk, reducing their availability for other biological functions, such as maintaining body mass, reproductive efficiency, and overall health (WEBSTER, 2005). A reliable indicator of metabolic disorders is the "downer cow" syndrome (CANALI et al., 2009). Heat stress, through reduced feed intake, survival rates, and nutrient absorption, negatively impact the energy balance of the organism, leading to weight loss in cows (TAO and DAHL, 2013). Reduced blood flow to the gastrointestinal tract caused by heat stress decreases epithelial nutrient absorption (ROLAND et al., 2016). All homeothermic animals respond to high temperatures by increasing heat dissipation and reducing heat production. This response includes increased lung ventilation, leading to a higher number of respiratory exchanges, sweating, decreased food intake, and loss of body fluids. As the respiration rate increases, the ventilation of catabolic CO2 also increases. Chronic hyperthermia leads to increased total volatile fatty acid production in the rumen and a decrease in ruminal pH, resulting in acute ruminal acidosis (KADZERE et al., 2002). Ruminal acidosis is also influenced by the reduced bicarbonate content in saliva (ZHAO et al., 2019). Dairy cows are at risk of rumen acidosis (SAMMAD et al., 2020) because rumen pH decreases due to the high concentration and accumulation of lactic acid. Low pH reduces the abundance of fibrolytic bacteria, causing a decrease in fiber digestibility (BAEK et al., 2020), and reduces rumen motility and rumination, which reduces the production of saliva as a buffering agent in the rumen (DAS et al., 2016), thereby reducing rumen pH. Meanwhile, only a few studies have evaluated the effect of HS on the rumen microbiome (KIM et al., 2020; PATRA and KAR, 2021). During heat stress, cows spend less time ruminating; however, if the feed contains a high starch content, a longer rumination period is observed (BRŠČIĆ et al., 2007). In addition to adequate feed and nutrient intake, limited access to or poor quality of water inevitably threatens the health and productivity of animals. Daily water requirements for cows depend on milk yield, feed intake, and ambient temperature (HÄBICH and KAMPHUES, 2009). On average, a cow requires 40 to 80 liters of water per day, but this can exceed 100 liters under high productivity, dry feed, and high ambient temperatures. The quality of water for cows must be the same as that for humans, and the hygiene of cow drinkers is also crucial (ALGERS et al., 2009).

Heat stress can also lead to lameness and laminitis in cattle. The contribution of heat stress to lameness is due to ruminal acidosis or increased bicarbonate excretion caused by accelerated mineral metabolism (COOK and NORDLUND, 2009). RHOADS et al. (2009) reported that the incidence of lameness in cows increases with rising air temperatures, prolonged standing, and discomfort while lying down. Lameness results in weakened hoof horn, ulcers, and hoof cracking, leading to the earlier culling of cows from the herd (RHOADS et al., 2009). As ambient temperature increases, the breathing rate rises until the animal begins open-mouth breathing-panting, which results from rapid CO_2 loss. The rise in ambient temperature affects the hypothalamic appetite center, leading to reduced food intake, weight loss, and the mobilization of body fat reserves during heat stress. Furthermore, food intake declines at air temperatures of 25-26°C in lactating cows and decreases more rapidly above 30°C; at 40°C, it can drop by as much as 40% (RHOADS et al., 2013). Ketosis, a metabolic disorder, occurs when an animal is in a severe state of negative energy balance, leading to intense liver fat accumulation and the build-up of ketone bodies in the blood due to incomplete fat catabolism. Fatty liver insufficiency is another consequence of the intense mobilization of fat from adipose tissue (BASIRICO et al., 2009). During heat stress, in addition to changes in adipose tissue, muscle tissue alterations are also present, leading to elevated plasma urea concentrations. Another indicator of muscle tissue catabolism is the concentration of 3-methylhistidine and keratin in the blood (BERNABUCCI et al., 2010).

Oxidative stress. Oxidative stress results from an imbalance between oxidant and antioxidant molecules and may depend on an excess of oxidants or a deficiency of antioxidants in the metabolism (AKBARIAN et al., 2016). Low antioxidant status in cows has been observed during the summer in both pre- and postpartum periods (MIRZAD et al., 2019). In lactating cows, increased levels of oxidants and decreased antioxidant molecules in the blood have been recorded during the hot summer season. Heat stress is associated with increased activity of antioxidant enzymes (superoxide dismutase, catalase, and glutathione peroxidase). Oxidative stress leads to an increase in reactive oxygen species in various cells and tissues, which negatively impacts normal physiology and metabolism. However, the body accumulates and protects itself with antioxidant molecules in the form of enzymes (superoxide dismutase, glutathione peroxidase, and catalase), non-enzymatic agents (albumin, L-cysteine, homocysteine, melatonin, and protein sulfhydryl groups), and low-molecular-weight antioxidants, such as vitamins (ascorbic acid, uric acid, alpha-tocopherol, beta-carotene, pyruvate, and retinol), which increase in response to temperature stress to protect against the harmful effects of altered oxygen forms. The loss of certain levels and consumption of glucose in tissues outside the mammary gland lead to lower milk synthesis in cows under heat stressors (GANTNER et al., 2020; BAUMGARD and RHOADS, 2013). As long as the body is in a state of oxidative stress, it results in various metabolic disorders in cows (ELSHAHAWY and ABDULLAZIZ, 2017). Furthermore, heat stress during the dry period (the last two months of gestation) reduces the proliferation of glandular tissue in mammary cells, thereby reducing milk yield in the subsequent lactation. Heat stress during the dry period also negatively affects the immune cells of cows before calving (TAO and DAHL, 2013).

Oxidative processes in the liver, when it produces ketone bodies that are reconverted into triglycerides, lead to increased production of free radicals, which undermine the body's antioxidant capacity. The production of free radicals increases with the progression of pregnancy in gestating cows, causing the body to undergo oxidative stress, resulting in metabolic disorders after calving (ELSHAHAWY and ABDULLAZIZ, 2017). In this regard, supplementation with antioxidants before and during heat stress reduces its intensity, decreases free radical production, and lowers cortisol levels, thereby improving conception rates in cows (MEGAHED et al., 2008). The more intense the oxidative processes in the liver, the greater the energy production (ATP), which in turn decreases stimulation of the appetite center, making heat stress more challenging for these animals and reducing production (WANKHADE et al., 2017).

Immunosuppression of the immune system. The sensitivity of ruminants to heat stress varies between species and breeds of domestic animals, and depends on the level of production (OHRAN et al., 2024; KADZERE et al., 2002; COLLIER et al., 2006), with differences in the animals' ability to reduce metabolic heat production. For example, animals adapted to warmer microclimates have lower metabolic rates and a greater capacity for heat dissipation. Increased sensitivity of cattle to heat stress is due to their high metabolic activity, compared to smaller ruminants, and a poorly developed mechanism for water retention in the kidneys and intestines (ROLAND et al., 2016).

The immune system represents a complex set of mechanisms for protecting animals from pathogenic invasion from the environment. Heat stress can weaken the immune system's function, particularly in lactating animals (LACETERA et al, 2013). Suppression of immune activity facilitates the occurrence of infections, which reduces reproductive efficiency, milk production, and animal welfare, and increases the use of antibiotics and antimicrobial resistance in microorganisms. LECCHI et al. (2016) report that high temperatures significantly impair the functionality of neutrophils, which play a central role in protecting the mammary glands from infections. Mastitis thus remains a major endemic disease in dairy cattle, typically occurring as an immune response to bacterial invasion. A two-year study on a dairy farm showed a higher risk of clinical mastitis in cows at the beginning of lactation during the month of July (VITALI et al., 2016).

Reduced milk production, heat stroke, and death. Heat stress significantly affects both the quantity and quality of milk produced in cows of all breeds, with the greatest impact observed in high-producing cows (SUMMER et al., 2018; NORDLUND et al., 2019; CHAVEZ et al., 2020; RAMÓN-MORAGUES et al., 2021; MIĆIĆ et al., 2022). This suggests a negative correlation between heat stress effects and milk yield per cow, whether measured daily or across the entire lactation period. GANTNER et al. (2011) reported that daily milk production in cows remains constant when ambient temperatures are low to moderate. However, as temperatures increase, milk production declines. Adverse environmental factors can lead to a reduction in milk production by 3-10%. HRISTOV et al. (2007) found that at a temperature of 35°C, milk yield decreased by 33%, and at 40°C, it decreased by 50%. The use of the temperature-humidity index (THI formula) is recommended to predict milk production declines in advance (EKINE-DZIVENU et al., 2020). The THI combines temperature and humidity into a single value and is considered a widely useful method for measuring the impact of microclimatic environmental conditions on milk production in cows (OUELLET et al., 2019; MAGGIOLINO et al., 2020; YAN et al., 2021). Research indicates that the most optimal thermoneutral THI value for cows is up to 57 (HALL et al., 2018; COLLIER et al., 2019), with higher values causing heat stress. The threshold for physiological adaptation to the harmful effects of heat stress starts at a THI value of 68, with 72 being defined as the threshold (THI - threshold) for lactating dairy cows (ANDERSON et al., 2013; ALLEN et al., 2015; VUČKOVIĆ et al., 2020). BERNABUCCI et al. (2010) demonstrated the decrease in milk production in cows on a daily basis, expressed in kilograms, depending on the THI level and the duration of exposure to the stressor. They found that mid-lactation milk production decreases by 35%, while at the beginning of lactation, it decreases by 14%. Milk yield is reduced by 0.88 kg per unit increase in THI level. In early lactation, cows require less feed because the body utilizes its reserves (nutrients for milk synthesis are drawn from tissues), whereas mid-lactation cows have significantly higher nutritional needs, leading to greater heat production, making the animals more susceptible to heat stress.

During any form of stress in cattle, central inhibition of milk ejection from the alveoli and udder cistern occurs, leading to incomplete emptying, which can result in pathological conditions, such as cisternal mastitis. In stressful situations, there is a connection between the nervous, endocrine, and immune systems. External stimuli perceived by the senses are transmitted through nerve impulses, activating the endocrine system (elevated levels of cortisol, β-endorphin, and adrenaline, and decreased levels of oxytocin in the blood). Prolonged activation of this system leads to a decline in immune response, and increased susceptibility to diseases. This indicates a link between central inhibition of milk ejection and stress, as well as a connection between endogenous opioids (β-endorphin) and catecholamines (adrenaline) in the central inhibition of milk ejection (BOBIĆ et al., 2011).

Table 1. The effect of heat stress on milk production in relation to THI index values (BERNABUCCI et al., 2010)

The level of heat stress in relation to the THI index	Temperature and relative humidity	Exposure time (h/day)	Reduction of milk yield (kg/h; kg/cow/day)
THI tolerance threshold (68-71)	22°C (72°F): 50%	4	0.283 kg/h -1.1 kg/cow/day
Mild to moderate THI (72-79)	25°C (77°F): 50%	9	-0.303 kg/h -2.7 kg/cow/day
Moderate to strong THI (80-89)	30°C (86°F):75%	12	-0.322 kg/h -3.9 kg/cow/day
Strong THI (90-99)	34°C (93°F): 85%	Not measured	

Prolonged exposure to high temperatures can lead to heat stroke, manifesting as exhaustion, muscle cramps and, eventually, organ dysfunction. These heat-induced complications arise when the body temperature of the animal increases by 3-4°C above normal. VITALI et al. (2015) indicate that summer mortality in dairy cows was higher during the daytime than at night during heat waves, and the risk of mortality remained elevated for three days after the heat wave ended. The mortality rate increased with the duration of the heat wave. When considering cow mortality by age, pregnant heifers and young cows up to 28 months old were not affected by heat waves, while all other age groups (29-60, 61-96, and >96 months) exhibited higher mortality rates.

CANALI et al. (2009) categorized cow diseases into several primary groups: respiratory diseases (cough, sneezing, nasal discharge, rapid breathing), digestive diseases (diarrhea, enteritis), eye diseases (eye discharge), reproductive diseases (metritis, mastitis, dystocia), and metabolic diseases (downer cow syndrome). The same authors noted that, in addition to disease occurrence, factors such as culling rates, expected lifespan, and mortality are also significant. An epidemiological study on dairy cows revealed that daily THI values of 70 and 80 represent the highest and lowest thresholds beyond which heat-induced mortality rates increase. The critical daily maximum and minimum THI values of 87 and 77, respectively, are thresholds above which the risk of heat-induced death becomes most severe (VITALI et al., 2015). As the sensitivity of cattle to higher THI values increases with milk production, a rise in milk yield from 35 to 45 kg/day increases heat stress sensitivity by 5%. The negative impact of heat stress in cows manifests within the first 24-48 hours, with THI values between 72-80 causing a significant reduction in milk production during the first four days after exposure (COLLIER et al., 2012).

The effects of climatic and microclimatic conditions on cattle reproduction

In addition to affecting milk production, heat stress has a detrimental impact on the reproduc- tive efficiency of cattle. Heat stress negatively influences the reproductive processes in females, by shortening the duration and intensity of estrus and increasing the frequency of anestrus and silent estrus. SINGH et al. (2013) reported that elevated levels of ACTH and cortisol inhibit estrus behavior induced by estradiol. High summer temperatures reduce follicular activity, delay ovulation, decrease the survival rate of the released oocyte, and lower the synthesis of sex hormones, such as estradiol in the follicular fluid. ROTH and HANSEN (2004) observed that follicular function improves during autumn, with undetected estrus rates of 76-82% during summer, compared to 44-65% in autumn and winter. Additionally, the pregnancy rate during the summer was only 27.4%, compared to 44% before the onset of heat stress. LACERDA and LOUREIRO (2015) found that heat stress reduces fertility by impairing the quality and functionality of oocytes and embryos, both directly and indirectly. The adverse effect of heat stress also extends to the development and maturation of oocytes, as reported by SINGH et al. (2013). Oocytes from heat-stressed cows lose their ability to fertilize (GENDELMAN and ROTH, 2012a) and develop to the blastocyst stage (GENDELMAN and ROTH, 2012b). Furthermore, periods of high temperatures lead to increased secretion of endometrial prostaglandin PGF-2α, threatening pregnancy maintenance, and causing miscarriages and infertility. Heat stress elevates FSH secretion due to reduced negative feedback inhibition from smaller follicles, while low progesterone secretion limits normal endometrial function and overall embryonic development (KHODAEI-MOTLAGH et al., 2011). ROTH et al. (2000) in their study show the immediate and delayed effects of heat stress on follicular dynamics, which are associated with high FSH, and at the same time low inhibin concentrations in plasma, which can be physiologically associated with low fertility in cattle during heat stress in summer. Exposure of post-implantation embryos (early organogenesis) and fetuses to heat stress leads to various teratogenic effects and defects (DEMETRIO et al., 2007). Fetal undernutrition and growth retardation have also been documented under heat stress conditions (TAO and DAHL, 2013). As parturition approaches, the maturation of the fetal hypothalamic-pituitary-adrenal axis causes an increase in adrenal mass and a subsequent rise in cortisol concentrations in both the fetus and the maternal blood. The last three to five days of fetal development are critical, with the highest cortisol concentrations, essential for the maturation of the fetal lungs and gastrointestinal tract, in lambs (ANTOLIC et al., 2015). AMUNDSON et al. (2006) also reported a significant reduction (P<0.01) in conception rates during summer (62%) and spring (44%) when the average minimum daily temperature and average daily THI values were equal to or exceeded 16.7°C and 72.9, respectively.

Bulls are crucial in reproduction under stringent selection criteria, making bull fertility equally, if not more, important for the fertilization of oocytes, ensuring a viable and genetically superior cattle production system. It is well established that a bull's testes must be 2-6°C cooler than his body temperature to produce fertile sperm. Thus, elevated testicular temperatures due to heat stress can alter the optimal sperm parameters and biochemical characteristics (DAS et al., 2016). Most studies have reported significant seasonal variations in semen characteristics (KUMAR et al., 2014; BHAKAT et al., 2014). RAHMAN et al. (2013) observed that sperm from summer ejaculates exhibited significantly reduced (P<0.01) fertility rates compared to control samples (53.7% vs. 70.2% and 81.5%). BHAKAT et al. (2014) noted optimal semen characteristics during winter, poor quality during summer, and intermediate traits during the rainy season, concluding that the hot, dry summer season negatively affects the biophysical properties of bull semen. The increase in THI during the summer months correlates with reduced feed intake, longer standing and moving times, and decreased reproductive performance in bulls. Brown Swiss bulls are more resilient to higher temperatures and relative humidity levels than Holstein Friesian and Simmental bulls (ATAKAN and VEYSEL, 2019). High air temperature and humidity impact cellular functions by directly altering and damaging various tissues or organs of the reproductive system in both sexes of domestic animals (DAS et al., 2016). Finally, all chronic stressors that trigger endocrine responses can lead to fetal morbidity and mortality (MOHANKUMAR et al., 2012).

The adaptation of cattle to adverse climatic and microclimatic conditions

The rise in ambient temperature triggers adaptive mechanisms within the physiological processes of the organism. Adaptation goes beyond mere tolerance to environmental conditions, it encompasses the organism's capacity to survive, grow, and reproduce under adverse influences (HOFFMANN and SGRO, 2011). Various adaptive mechanisms allow animals to adjust to changing climatic and microclimatic conditions, including genetic or biological adaptation, phenotypic or physiological adaptation, acclimatization, and habituation. Factors influencing an animal's response to stress include the intensity of the stressor, prior experiences, physiological status, and more (GAUGHAN, 2012).

Climatic adaptation, known as acclimatization, involves changes in the rate of hormone secretion and the number of receptors in target tissues. Consequently, biochemical processes in the liver, adipose tissue, muscle, and bone tissue are altered (INGVARTSEN, 2006). Acclimatization to heat stress is achieved through modifications in homeostasis, where control and endocrine adaptation mechanisms operate on the basis of homeorhetic principles. BEN SALEM (2011) describes acclimatization as a homeorhetic process, regulated by the endocrine system. Hormones involved in adaptation to heat stress include thyroid hormones, prolactin, glucocorticoids, and mineralocorticoids. Cows adapted to heat stress exhibit lower glucocorticoid concentrations, and cortisol (released during heat stress) has been shown to activate the genes responsible for stress adaptation (ANTOLIC et al., 2015). Thyroid hormones play a crucial role in thermogenesis, with their concentrations inversely correlated with body heat. Higher concentrations of these hormones initiate thermogenic processes in the body (PERIC et al., 2013).

The mineral composition in the body is critical for proper prenatal and postnatal development of calves, and their tolerance to environmental stressors. Calcium and phosphorus concentrations are vital for bone mineralization, which later contributes to greater stress tolerance in calves (OHATA et al., 2016). Among dairy livestock species, goats are the most adapted to heat stress, outperforming cows in terms of production, reproduction, and disease resistance (KUMAR et al., 2014; SILANIKOVE and KOLUMAN, 2015). MYLOSTYVYI et al. (2021) report that Brown Swiss cattle are more resistant to high ambient temperatures compared to Holstein Friesian and Simmental breeds.

This complex interplay of hormonal regulation, mineral balance, and genetic predisposition underscores the multifaceted nature of cattle adaptation to climate and microclimate stressors. Adaptation not only ensures survival, but also supports continued productivity and reproductive efficiency, even under challenging environmental conditions.

The behavior of cows in response to adverse climatic and microclimatic conditions

The relationship between climate change and the neuroendocrine system of animals typically alters all forms of behavior, including instinctual drives related to the inheritance of favorable traits in the next generation (BAUMGARD and RHOADS, 2013). During heat stress, there are fundamental behavioral changes, such as seeking shelter, altering body position (standing/lying down), reducing locomotion during the hottest parts of the day, and seeking shade behind other animals (ROLAND et al., 2016).

Every farm structure is unique in terms of its construction and exposure to environmental influences, and requires different solutions (BAKONY and JURKOVICH, 2020, CARDOSO et al., 2021). SILANIKOVE and KOLUMAN (2015) indicated that the severity of heat stress is expected to increase in the future due to the progression of global warming, leading to elevated body temperature, and increased respiratory rate, heart rate, and rectal temperature. These physiological changes, in turn, negatively impact the productive and reproductive efficiency of animals. KADOKAWA et al. (2012) reported that a rectal temperature (RT) greater than 39.0°C and a respiratory rate (RR) exceeding 60/min indicate that cows are already experiencing heat stress sufficient to reduce milk yield and fertility. As the average global temperature continues to rise, the harmful effects of ecological stress on animal welfare and production will intensify (BERNABUCCI, 2019).

Genetic predispositions (LUO et al., 2021), technology, and farm management practices can mitigate some of the conditions leading to heat stress in cows (WANG et al., 2020). This highlights the importance of adapting both the genetic selection and the environmental management of livestock, to withstand the challenges posed by climate change better, ensuring sustained productivity and animal welfare in increasingly stressful conditions.

Conclusions

In conclusion, the imbalance between metabolic heat production within the animal's body and its dissipation into the environment leads to heat stress under high ambient temperatures. Initial responses of animals to heat stress include increased respiration rate, elevated body temperature, and higher heart rate, directly resulting in reduced feed intake, increased water consumption, slower growth rates, decreased milk yield and quality, impaired reproductive performance, and the development of inflammatory and disease conditions, with severe cases potentially leading to mortality. Dairy breeds are particularly susceptible to heat stress compared to other breeds, as well as animals with higher production performance, due to their increased metabolic heat production, which complicates its dissipation.

Heat stress suppresses the immune and endocrine systems, thereby increasing the animal's vulnerability to various negative agents, pathogens, and diseases. While the animal's organism has a limited ability to become accustomed to and capacity to adapt to thermal effects (acclimatization and adaptation to heat stress), this is insufficient for the rapid pace of current climatic changes. Therefore, this continues to pose sustainable agriculture and dairy production significant challenges in the face of global climatic changes and environmental heat stress.

This review underscores the urgent need to develop and implement effective strategies to mitigate the impacts of heat stress on cattle. It highlights the importance of understanding the physiological, behavioral, and genetic mechanisms of adaptation, and emphasizes the role of management practices and technological innovations in enhancing resilience. Addressing these challenges is critical for ensuring the welfare, productivity, and long-term sustainability of cattle farming amidst ongoing climate change.

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SAŽETAK

Toplinski stres znatna je prijetnja za mliječna goveda jer utječe na njihovu fiziološka, reproduktivna i proizvodna svojstva. Ovaj pregledni rad ima za cilj pružiti detaljnu analizu učinaka toplinskog stresa na mliječna goveda, s naglaskom na to kako povišene temperature okoliša utječu na proizvodnju mlijeka, reproduktivnu učinkovitost i opće zdravlje životinja. Raspravlja se o fiziološkim odgovorima na toplinski stres, uključujući povećanu brzinu disanja, povišenu tjelesnu temperaturu i promjene u ponašanju pri hranjenju i pijenju. Toplinski stres dovodi do smanjenja unosa hrane, povećanja konzumacije vode, smanjenja brzine rasta te smanjenja prinosa i kvalitete mlijeka. Reproduktivne odlike također su promijenjene, što je praćeno sa smanjenom plodnošću i povećanim rizikom od gubitka embrija. Mliječne pasmine krava, osobito one s vrlo visokim prinosom, osjetljivije su na toplinski stres zbog veće proizvodnje metaboličke topline. Nadalje, ovaj rad ističe utjecaj toplinskog stresa na imunosni i endokrini sustav, povećavajući ranjivost životinja na bolesti i upalna stanja. S obzirom na ograničenu sposobnost životinja da se prilagode brzom tempu klimatskih promjena, ovaj pregledni rad naglašava potrebu za učinkovitim strategijama upravljanja, uključujući promjene u okolišu i genetsku selekciju, kako bi se ublažili nepovoljni učinci toplinskog stresa. U konačnici, održiva proizvodnja mlijeka ostaje znatan izazov u kontekstu globalnih klimatskih promjena i rastućih temperatura.

Ključne riječi: toplinski stres; mliječna goveda; fiziološki odgovori; proizvodnost; ponašanje životinja