Influence of Heat Stress on Some Physiological, Productive and Reproductive Indicators in Dairy Cows – A Review

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Abstract. *The purpose of this review is to examine the scientific literature on the effects of heat stress on some physiological, productive and reproductive parameters in dairy cows. The article analyzes the scientific papers in which the influence of heat stress and its impact on some indicators is studied. As a result of the review, it became clear that heat stress has an impact on the studied indicators, but there are no clear criteria at which values of temperature-humidity index (THI) this effect is registered. The relationship between heat stress, productivity, successive lactation and physiological and reproductive parameters in dairy cows is still controversial. This poses a challenge, through research, to solve the problems in regards to high temperature and animal welfare and productivity for specific climatic conditions.*

Introduction

Heat stress in dairy cows is considered to be a combination of environmental factors that cause an increase in body temperature and a number of other reactions.

Temperature and humidity are considered to be the main indicators of the environment. There are other additional environmental factors such as air velocity and solar radiation that affect the cooling of cows under heat stress. In order to take into account the impact of all these meteorological conditions and their impact on the formation of heat stress, indices have been developed to measure the value of this stress.

As a result of heat stress in the body of cows, a number of physiological changes are observed. The main ones are changes in body temperature, respiratory rate, heart rate, digestive changes, hormonal reactions and reactions in the acid-base balance of the body. Under the influence of heat stress and the physiological-adaptive processes in cows, there are changes in the quantity and quality of milk produced, as well as a number of reproductive changes, usually associated with deterioration of reproductive performance under heat stress.

Despite many studies on the topic of heat stress in dairy cows, research continues to this day. Data on the impact of heat stress on dairy cows varies, as they are conducted in different parts of the world, characterized by the specifics of climatic characteristics, as well as some individual characteristics of reared cows, such as breed, productivity and others.

All this makes the issue of heat stress relevant, given the search for an adequate response and addressing its consequences.

Heat stress in modern cattle breeding

Heat stress is defined as a set of external forces that act directly on the animal's body, causing an increase in body temperature and inducing a series of adaptive responses (Dikmen and Hansen, 2009). The steady rise in temperatures and global warming (Schär et al., 2004), combined with the significant increase in the number of productive animals and the intensification of cattle breeding (Renaudeau et al., 2012), make heat stress a great challenge and a problem for modern farmers. Given the normally high heat loads in productive dairy cows caused by the large amount of energy used for milk production and other physiological needs (Chebel et al., 2004), high temperatures and humidity can significantly contribute to deterioration in the health status of animals and impairment of their comfort (West, 2003). Not surprisingly, the problem of heat stress is most common in geographical areas where the summer season is long and prolonged exposure to sunlight and high humidity is established (Schüller et al., 2014). Animals located in northern geographical areas may also be exposed to heat stress, where the summer season is shorter but hot enough and there is a minimal drop in temperature during the dark part of the day. Heat stress leads to significant economic losses for farmers, deteriorating many productive, reproductive and health indicators in cows.

Environmental parameters influencing as a risk factor for heat stress

Cows are able to adapt to changing temperature and

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humidity conditions throughout the year (Kadzere et al., 2002). This is confirmed by the relatively wide range of thermo-neutral conditions found in cattle. Temperature fluctuations in the range of –0.5–20.0°C and 60–80% relative humidity (West, 2003) are generally accepted as a thermo-neutral value that does not significantly affect the normal physiology of animals. Berman et al. (1985) claim that the upper limit of the air temperature at which the basic body temperature in cattle can be maintained is 25.0–26.0°C.

Air temperature and relative humidity are considered to be the most important factors that determine the heat exchange between the animal's body and the environment. Other important elements of the microclimate – such as air movement and sunlight – also play a significant role in inducing a heat stress response in animals (West, 2003; Da Silva et al., 2010). Changes in air velocity affect convection cooling in cows (Davis and Mader, 2003). The recommended air velocity for dairy cattle in the United States during heat stress is 1.8 to 2.8 m/s (Bailey et al., 2016). Berman (2005) believes that air velocity is lower when cows move in the barn, so measurements do not always reflect real values. This is in line with the study of Herbut (2013) and Hempel (2018), which indicated the need for measurements in the entire area where the cows are housed, and not just in individual points. Kadzere et al. (2002) note that during the hot months, maintaining an air velocity above 1.0 m/s at high humidity (e.g., by means of sprayers) significantly cools the animal's body.

Solar radiation is one of the leading environmental factors affecting ruminants (Schutz et al., 2009). Radiation includes both direct radiation from the sun and diffuse radiation received from the sky and/or reflected from clouds (Da Silva et al., 2010). The effects of radiation, whether direct, diffuse or reflected, can be a major determinant of the environmental conditions in which cows are reared, mainly in grazing (Schutz et al., 2008; Tucker et al., 2008). Studies conducted in free barns show significant differences in microclimate conditions. These variations are the result of the higher air temperature and litter surface observed during the day in boxes adjacent to walls that are exposed to direct sunlight compared to those in the shade (Angrecka and Herbut, 2016).

Many environmental indices have been proposed, which are used to measure meteorological conditions. Examples are the THI, the Black Globe-Humidity Index (BGHI) and the Environmental Sustainability Index (ESI). The situation with heat stress has been shown to worsen when high relative humidity is observed at high air temperatures in the animal environment (Hill and Wall, 2015; Herbut et al., 2018 b). Over the years, two main methods have been developed to assess environmental risk factors and animal responses to changing environmental conditions. The first of them is a variety of different indices of temperature and humidity, expressed in absolute values, which determine the thermal comfort of animals. The second includes algorithms expressed in °C. The indices have undergone many modifications and include different ranges of values that determine the threshold levels of heat stress in dairy cows.

Physiological changes in the body of animals that are affected by the effects of heat stress

Body temperature

The body temperature of cows under thermo-neutral conditions is maintained by the thermoregulatory system in the range of 38 to 39.2°C (Ammer et al., 2016). Under these conditions, the heat exchange in the animal's body (through cell and vascular membranes) and the heat exchange with the environment are balanced. This process is almost always dynamic (Taylor et al., 2014).

When the ambient temperature is elevated, mechanisms are activated in the body that aim to maintain the homeostasis and temperature status of the animals or to regulate them within acceptable physiological limits (Werner et al., 2008). The mechanisms that release excess heat from the body are regulated by the hypothalamus. It receives information about fluctuations in body surface temperatures and deeper tissues from receptors located on them. Under temperature stress, a rapid response is induced, initiated by skin receptors. As a result, the central nervous system, the endocrine system and peripheral components of the autonomic system are activated (Colier et al., 2012).

When thermoregulatory mechanisms prove insufficient to dissipate external heat, body temperature rises. At values > 39.4°C, a state of hyperthermia occurs. Nowadays, temperature changes on the surface of the body as well as in the internal body temperature can be easily monitored using non-invasive methods such as thermography (Godyń et al., 2013; Hoffmann et al., 2013; Unruh et al., 2017 , Hristov et al. 2021a; Hristov et al. 2021b) or small wireless sensors (Lees et al., 2018). Cattle body temperature can be measured in various parts of the body, such as the abdomen, ear canal and vagina, but the most common method of assessing internal body temperature is to measure rectal temperature. Lemerle and Goddard (1986) found that rectal temperature began to rise at THI values > 80. Collier et al. (2006) found that cows reared in shady areas had a rectal temperature 0.5°C (38.9 to 39.4°C) lower than cows exposed to direct sunlight without shade access.

Respiratory rate

Sweating and panting are considered to be the first and main reactions of animals to temperature stress. Collier et al. (2012) reported that the body of animals is in the acute phase of response to heat stress when the skin temperature reaches 35°C and the respiratory rate is 60–70 dd/min. Lemerle and Goddard (1986) found that the respiratory rate began to increase gradually, at THI > 73, and significantly rapidly at THI > 80. It has been proven that the value of this physiological parameter depends on the amount of shade and cooling in the area where the cows are raised, their age and the time they spend in an upright and lying position. In adult cows, a respiration rate of up to approximately 80 breaths per minute has been observed (Stevens, 1981). In addition, Collier et al. (2006) found that cows kept in shady areas had a respiratory rate of 54 breaths per minute, while cows without access to shading had 82 breaths per minute. Similar results were reported by Eigenberg et al. (2005), whose studies found about 16 rpm more in cows raised without access to shady areas. Cows reared in free barns with a cooling system showed a reduction in the number of breaths per minute from 95 to 57 (West, 2003). Based on studies conducted in the afternoon, Chaiyabutr et al. (2008) found that cows kept in refrigerated rooms made 64 breaths per minute, while cows in uncooled areas made 86 breaths per minute.

Heart rate

When the animal's body is exposed to heat, cardiac output increases. While the stroke volume is maintained or slightly increased, the heart rate accelerates significantly and is the main driving force behind this process (Johnson and Proppe, 1996). Control and regulation of the heart rate in heat stimuli may be a consequence of direct irritation of high temperature on the sinoatrial node and the sympathetic and parasympathetic nerve endings of the heart (Wilson and Crandall, 2011). Kovács et al. (2018) found that Holstein calves reared in conditions of extreme heat load without shade have a higher heart rate than calves kept in the shade. Similar results are shared by Bun et al. (2018) in a study of dairy cows. Dalcin et al. (2016) found that at a BGHI value of 72, the heart rate began to increase linearly in dairy cattle.

Digestion and absorption of nutrients

Digestion is influenced by various factors, such as the time the animals consume the food, the quality of the food, the composition of nutrients, the rate at which nutrients pass through the digestive tract and the volume of the digestive organs (Ellis et al., 1984). All these factors are affected by heat stress. At high temperatures, reduced food intake leads to increased digestive processes by slowing the movement of food in the proventriculus and increasing the volume of the rumen (Lippke et al., 1975). These physiological changes are more pronounced in animals that consume more feed.

Peripheral vasodilation and central vasoconstriction lead to a reduced blood flow to the proventriculus of ruminants (Engelhardt et al., 1977). This in turn reduces the plasma flow through the portal vein, which inhibits nutrient absorption (McGuire et al., 1989).

Influence of heat stress on hormones in dairy cows

The endocrine system, which is a major link in the coordination of metabolism, changes significantly when animals are under heat stress (Beede et al., 1986). Hormones associated with adaptation to heat stress are prolactin (PRL), growth hormone (GH), thyroid hormones, glucocorticoids, mineralocorticoids, atecholamines, and antidiuretic hormone (ADH). Prolactin is vital for mammogenesis (Buttle et al., 1979), lactogenesis (Akers et al., 1981) and to varying degrees for galactopoiesis (Wilde et al., 1996). Plasma PRL concentrations increase during heat stress in dairy cows (Wetteman et al., 1979). Collier et al. (1982) suggest that increased PRL is associated with increased water and electrolyte requirements when animals are exposed to heat stress.

Growth hormone is produced in the anterior pituitary gland. It does not perform its functions through the target gland, but exerts its effect on almost all tissues of the body. Plasma GH levels decreased from 18.2 ng/mL in thermo-neutral environments to 13.5 ng/mL in heat stress in Jersey cows (Mitra et al., 1972). Igono et al. (1988) reported that the GH content in the milk of low, medium and high productive groups of cows decreased when the THI exceeded 70. A decrease in plasma GH was not observed in cows reared in thermo-neutral conditions subjected to the same diet (McGuire et al., 1989). Decreased GH hinders the formation of energy used for heat production in the body of animals (Bauman et al., 1980). GH also promotes heat production by stimulating thyroid activity (Yousef et al., 1966). Therefore, decreased secretion of the growth hormone is more than a physiological response necessary for the survival of homothermic animals at high ambient temperatures.

The thyroid gland secretes triiodothyronine (T3) and thyroxine (T4). These hormones are essential for the regulation of metabolism and have a positive correlation with weight gain and tissue formation (Magdub et al., 1982). The response of T3 and T4 to heat stress is slow and it takes several days to reach a constant level of concentration (Silanikove, 2000). A decrease in plasma T3 concentrations from 2.2 to 1.16 ng/mL was reported by Johnson et al. (1988). This decrease in thyroid hormones together with the decreased level of GH in plasma has a synergistic effect in the body's desire to reduce heat production (Yousef et al., 1966).

Acute and chronic heat stress lead to various changes in glucocorticoid concentrations. Alvarez and Johnson (1973) reported an increase in glucocorticoid levels from 2.4 to 3.9 μg/100 mL (62%) by the second hour of heat exposure, reaching a peak of 5.4 μg/100 mL (120%) at the 4th hour, then gradually decreasing to the norm of 2.4 μg/100 mL at the 48th hour, maintaining this concentration despite the continuing thermal irritant. The initial increase in plasma glucocorticoids is due to the activation of an adrenocorticotropin-releasing mechanism (ACTH) in the hypothalamus by skin thermoreceptors (Chowers et al., 1966), while a later decrease to normal, despite continued thermal irritation, shows negative feedback between increasing glucocorticoid concentrations and reporting a decrease in glucocorticoid-binding transortin (Lindner, 1964). Glucocorticoids act as vasodilators, promoting heat loss. They have a stimulating effect on proteolysis and lipolysis, thus providing energy to the animal, compensating for reduced food intake (Cunningham and Klein, 2007).

The relationship between heat stress, plasma aldosterone concentration and urinary electrolyte excretion has been documented by El-Nouty et al. (1980). Plasma aldosterone concentrations remained unchanged during the first few hours of heat exposure. However, with prolonged exposure, it is 40% lower and decreases rapidly in the following hours. This decrease in aldosterone levels is due to a decrease in serum K levels as a result of increased sweat excretion (El-Nouty et al., 1980) and is explained by the large difference between ruminants and non-ruminants in terms of Na and K during heat stress. Non-ruminants excrete sweat with high Na concentration and low K concentration (Lippsett et al., 1961); unlike ruminants, in which the opposite is true. The concentration of catecholamines increases in both acute and chronic heat stress. Alvarez and Johnson (1973) reported an average increase of 45% and 42% for short and 91% and 70% for long heat exposure for adrenaline and noradrenaline, respectively. Allen and Bligh (1969) reported that catecholamines activate the sweat glands and participate in the regulation of their activity.

Increased plasma osmolarity and decreased blood volume lead to secretion of ADH by the pituitary gland, which in turn acts on the kidneys, leading to water retention (Cunningham and Klein, 2007). Increased loss of water through the airways and skin of heat-stressed animals results in increased secretion of ADH, which is intended to retain water in the body and increase its intake (El-Nouty, 1980).

Acid-base balance and heat stress

Cows subjected to heat stress usually show changes in acid-base balance as a result of physiological reactions accompanying the cooling of the body. Frequent respiratory activity and sweating increase in proportion to the body's need for cooling. Accelerating respiration increases CO2 loss through pulmonary ventilation, reduces the concentration of carbonic acid in the blood and upsets the balance with bicarbonate, which changes the pH of the blood and leads to respiratory alkalosis (Benjamin, 1981). Compensation for respiratory alkalosis includes increased urinary excretion of bicarbonate (Benjamin, 1981), which leads to a decrease in its concentration in the blood.

Influence of heat stress on productive indicators

Amount of milk

Lactating cows are more sensitive to heat stress than dry cows. This is due to milk production, which significantly speeds up metabolism (Purwanto et al., 1990). In addition, due to the positive relationship between milk production and heat production, cows with higher milk yields are more prone to heat stress than animals with lower milk yield (Spiers et al., 2004). When a cow is under heat stress, adaptive mechanisms are activated that reduce the nutrients used for milk synthesis (West, 2003; Rhoads et al., 2009). At the same time, it speeds up the metabolism caused by the activation of the thermoregulatory system. Under mild to severe heat stress, the requirements for maintaining a normal metabolism can increase from 7 to 25% (NRC, 2001), which can lead to a significant decline in milk production. Reduced milk production is often used in various studies as an indicator of reduced welfare of animals that are already susceptible to diseases such as mastitis (Gröhn et al., 2004). Rushen et al. (2001) reported that milk yield decreased instantaneously when cows were exposed to a stressful or unfamiliar environment. In this regard, it is often accepted that milk production can be interpreted as a direct indicator of animal welfare and can be used by farmers as a way to assess the condition of cattle in changes in their environment (e.g., increase in ambient temperature or changes in diet). Others have challenged milk production as an acceptable indicator of well-being (von Keyserlingk et al., 2009), especially in cows exposed to heat stress. The reason is the delay in registering a decline in milk production after the animals have already been exposed to high ambient temperatures. Collier et al. (1981) reported a delay of 24 to 48 hours from an increase in ambient temperature to a decline in milk production. Additional evidence provided by Linvill and Pardue (1992) indicates that milk production only begins to decline when the THI consistently exceeds 74 for the previous 4 days. From this, it is clear that if changes in milk production are detected only on days after which the animals have already been under heat stress, this measure is limited and at best indirect to assess the welfare of cattle (von Keyserlingk et al., 2009). Despite the identified barriers to the use of milk production as an indicator of welfare in dairy cows, recent data suggest that changes in milk composition may be far more useful in assessing the condition of animals exposed to immediate heat stress (Hu et al., 2016).

Relationship between heat stress, dry matter intake and milk production

Many scientific publications show a link between the occurrence of heat stress and reduced dry matter intake (DMI), as this is an immediate adaptive response in animals (Kadzere et al., 2002; West, 2003; Rhoads et al., 2009). The reduced productivity of the animals during heat stress is explained only by parts with reduced DMI. Baumgard et al. (2011) claim that lower consumption of heat-stressed cattle explains only 35–50% of the decline in milk yield. According to Slimen et al. (2016), heat stress causes a reorganization in the use of body resources such as fat, protein and energy. Post-absorption metabolism is altered, and this occurs regardless of the decline in food intake (Slimen et al., 2016). Noordhuizen and Bonnefoy (2015) found a decrease in milk production of 600–900 kg of milk per lactating cow and a decrease in feed intake with 0.85 kg DMI per cow less for each 1° increase in ambient temperature C (West, 2003). According to Kadzere et al. (2002), DMI in cows can report a decrease of up to 40% when the ambient temperature exceeds 30°C, which leads to a deterioration of the energy balance. According to research by Bouraoui et al. (2002), increasing the value of THI from 68 to 78, leads to a decrease in DMI by up to 9.6%. In West's study (2003), food intake began to decline one day after the onset of heat stress. In addition, West (2003) found a decrease in milking 2 days after the animals were under heat stress. The study by Herbut et al. (2018), conducted in free barns, also revealed a 2- to 4-day delay before a decline in milk production was found. Studies show that the decline in milk production depends on both the strength of the heat wave and the length of previous warm periods. The large number of hot days in July and August leads to a rapid response of animals to subsequent changes in thermal conditions in the coming months (Herbut et al., 2018a).

Relationship between heat stress, water intake and milk production

Water intake is extremely important for dairy cattle. For cows producing 41.5 kg of milk per day under thermo-neutral conditions, the water intake is about 135 kg per day (Kadzere et al., 2002). Variations in water intake are closely related to DMI and milk yield, ambient temperature, and relative humidity (Cardot et al., 2008). Water for the animals must be provided in appropriate quantities and temperatures. A 10% decrease in the body's water supply in cows can adversely affect milk production (González Pereyra et al., 2010).

Quality composition of milk

Results from studies by various authors (Bouraoui et al., 2002; Hammami et al., 2013) also report a direct link between heat stress and deterioration in milk quality. Poor temperature and humidity conditions lead to an increase in the number of somatic cells in milk and a decrease in fat and protein (Hammami et al., 2013; Lambertz et al., 2014). As THI increases, so does the number of somatic cells.

Lipids are one of the main components of milk. The dominant fraction of milk fat is TAG (about 98%), present in the form of fat globules (Mansson, 2008). In addition to being an energy source, the composition of TAG is important for human health and the properties of dairy products (Jensen, 2002; Palmquist, 2006). The second most important fraction of milk fat are polar lipids, which are a major structural element of the membrane of fat globules and thus play the role of emulsifier, ensuring the stability of the milk emulsion system (Fong et al., 2007, Sánchez-Juanes et al. 2009). The main classes of lactic polar lipids include phosphatidylcholine (PC), phosphatidylethanolamine (PE), phosphatidylserine (PS), phosphatidylinositol (PI), sphingolinositol (PI), sphingomylyscholine LP, lactosylceramide (GC) and laczylceramide (2002).

By correlating the meteorological data with the characteristics of fatty acids (FA), it was found that an increase in THI shows a decrease in the content of short-chain and medium-chain fatty acids and an increase in long-chain (Hammami et al., 2015). A similar conclusion was made in other studies of heat-stressed cows (Lacetera et al., 2003). However, these results have not always been convincing, as the effect of heat stress is often confused with different eating patterns over the seasons. Regarding the effect of heat stress on the TAG profile and polar lipid composition, no information is available.

Influence of heat stress on reproductive indicators

The decline in the number of cows bred during the summer season can vary between 20 and 30%, despite the presence of animals that clearly show estrus (De Rensis and Scaramuzzi, 2003). High ambient temperatures have a negative effect on a cow's ability to behave naturally during heat, as it reduces the duration and intensity of estrous expression (Orihuela, 2000). The reason for this is considered to be the reduced intake of dry matter and the subsequent disturbance in the production of hormones (Westwood et al., 2002). An additional reason is the desire of man to turn cows from a "seasonal" to a "year-round" breeding unit. The adverse effects of heat stress on the reproductive cycle are year-round, but significantly more severe during the summer months. Hansen and Aréchiga (1999) report reduced estrus in heat-stressed dairy cows. These authors believe that heat stress causes physical lethargy, which acts as an adaptive mechanism that limits the additional heat production of the animal already generated by activities during estrus. Additional evidence suggests that jumps as an indicator of estrus in beef cattle are significantly less in summer than in winter (White et al., 2002). A shorter duration of estrus is found when European breeds move to the tropics, with differences in climate and nutrition (Orihuela, 2000). Reproductive indicators are often used as an indicator of well-being in heat-stressed cows, as problems with animal breeding (De Rensis and Scaramuzzi, 2003), ovum quality disorders (Roth et al., 2001) and abortion or early embryonic mortality (Silanikove, 2000) are common during these periods. However, these indicators are retrospective in nature and only give us information that the animal was already in a state of stress. Therefore, these data are of greater value in the management of future nurseries and as a means of determining the need to implement improved strategies to combat heat stress. A more accurate and useful indicator for assessing well-being is measuring the rectal temperature on the day of insemination. Pereira et al. (2013) reported that the chance of fertilization up to 60 days registered a decrease from 21% to 15% at a rectal temperature higher than 39.1°C found during artificial insemination.

Heat stress alters the reactions along the hypothalamic-pituitary-ovarian axis

Because the main hormones that regulate ovarian function are gonadotropin-releasing hormone from the hypothalamus and gonadotropins, luteinizing hormone (LH) and follicle-stimulating hormone (FSH) from the anterior pituitary gland, some authors have investigated the effect of heat secretion on stress. Changes in LH concentration under the influence of heat stress in the peripheral blood are intermittent. Some studies report unchanged concentrations (Gwazdauskas et al., 1985; Gauthier, 1986), while others report an increase (Roman-Ponce et al., 1981) and reduced concentrations (Madan and Johnson et al., 1973; Wise et al., 1988; Gilad et al., 1993; Lee, 1993). Regarding the model of LH secretion in cows subjected to heat stress, there is a decrease in the amplitude of the LH pulse (Gilad et al., 1993) and LH pulse, as well as in their frequency (Wise et al., 1988). The effect of heat stress on the LH preovulatory peak is also controversial: a decrease in the endogenous LH peak from heat stress has been reported in heifers (Madan and Johnson, 1973) but not in cows (Gwazdauskas et al., 1981; Gauthier, 1986; Rosemberg et al., 1981). The reasons for these discrepancies are unclear. These differences are thought to be related to preovulatory estradiol levels, as the amplitude of tonic LH impulses and the GnRH-induced preovulatory plasma peak of LH are lower in cows with low plasma estradiol concentrations but not in cows with high plasma concentrations of estradiol (Gilad et al., 1993). Plasma inhibin concentrations in summer are lower in heat-stressed cows (Wolfenson et al., 1995), which may reflect impaired folliculogenesis, as a significant proportion of plasma inhibin comes from small and medium-sized follicles. Plasma FSH concentrations are higher during the preovulatory period in summer; this is associated with lower circulating concentrations of inhibin (Ingraham et al., 1974).

Influence of heat stress on gametogenesis and embryo

Gametogenesis is sensitive to temperature changes. Normal spermatogenesis requires a temperature that is below normal body temperature. Recent evidence suggests that oocyte development is also sensitive to temperature (Rutledge et al., 1999). The negative effects of heat stress on fertility may be the result of the direct effect of high temperatures on the ovaries and the quality of oocytes, respectively.

The intrauterine environment is also compromised in cows that are subjected to heat stress; decreased blood flow to the uterus and increased temperature (Roman-Ponce et al., 1978; Gwazdauskas et al., 1975). These changes inhibit embryonic development (Rivera and Hansen, 2001), increase early embryonic death, and lead to unsuccessful inseminations. The high ambient temperature indicates a negative effect on the embryos in the pre-attachment stage (Ray et al. 1992), but the degree of this effect decreases gradually with the development of the embryo (Ealy et al., 1993). Heat stress can affect the endometrium of the uterus, leading to premature secretion of prostaglandins (Putney et al., 1989), followed by luteolysis and fetal loss. Most often, embryonic death occurs by the 42nd day.

Influence of heat stress on the development of follicles

Heat stress slows follicle expression and prolongs follicular wave, leading to adverse effects on oocyte quality (Roth et al., 2001; Badinga et al., 1993) and follicular steroidogenesis (Roth et al., 2001; Howell et al., 1994; Palta et al., 1997). Heat stress suppresses the development of dominant follicles, which causes more medium-sized follicles to survive (Wolfenson et al., 1995; Roth et al., 2000; Wilson et al. 1998; Vasconcelos et al., 1998; Badinga et al., 1993). Thus, the duration of preovulatory follicle dominance increases in summer, which in heifers is negatively related to fertility (Mihm et al., 1994). When the expression of an individual dominant follicle is suppressed, it is possible to develop more than one dominant follicle, which is reflected in twins, which can often be observed in summer (Ryan et al., 1991).

Conclusion

As a result of the review, it became clear that the topic of heat stress and its impact on dairy cows has been widely studied in many parts of the world. Despite the many data from various authors, there is still no unanimous opinion on which indices are the most accurate and at which values of the temperature-humidity index measures need to be taken. Particularly interesting is the question of the adaptability of dairy cattle to heat stress and its effects on their physiological, productive and reproductive indicators. Following the review, it is clear that research on the issue is likely to continue in order to find adequate solutions to the issue of heat stress and its impact on dairy cows.

References

1. Ammer S., Lambertz C., Gauly M. (2016). Comparison of different measuring methods for body temperature in lactating cows under different climatic conditions. J. Dairy. Res., 83: 165–172.
2. Angrecka S., Herbut P. (2016). Impact of barn orientation on insolation and temperature of stalls surface. Ann. Anim. Sci., 16: 887–896.
3. Akers, R.M., D.E. Bauman, A.V. Capuco, G.T. Goodman and H.A. Tucker, 1981. Prolactin regulation of milk secretion and biochemical differentiation of mammary epithelial cells in periparturient cows. Endocrinology, 109: 23-30.
4. Allen, T.E. and J. Bligh, 1969. A comparative study of the temporal patterns of cutaneous water vapor loss from some domesticated mammals with epithelial sweat glands. Comp. Biochem. Physiol., 31: 347.
5. Alvarez, M.B. and J.D. Johnson, 1973. Environmental heat exposure on cattle plasma catecholamine and glucocorticoids. J. Dairy Sci., 56: 189-194.
6. Bailey T., Sheet s J., McClary D., Smith S., Bridges A. (2016). Heat Abatement. Elanco.
7. Baumgard L.H., Wheelock J.B., Sanders S.R., Moore C.E., Green H.B., Waldron M.R., Rhoads R.P. (2011). Post absorptive carbohydrate adaptations to heat stress and monensin supplementation in lactating Holstein cows. J. Dairy Sci., 94: 5620–5633.
8. Berman A. (2005). Estimates of heat stress relief needs for Holstein dairy cows. J. Anim. Sci., 83: 1377–1384.
9. Berman A., Folman Y., Kaim M., Mamen M., Herz Z., Wolfenson D., Arieli A., Graber Y. (1985). Upper critical temperatures and forced ventilation effects for high yielding dairy cows in a sub-tropical climate. J. Dairy Sci., 68: 1488–1495.
10. Bouraoui R., Lahmar M., Majdoub A., Djemali M., Belyea R. (2002). The relationship of temperature-humidity index with milk production of dairy cows in a Mediterranean climate. Anim. Res., 51: 479–491.
11. Badinga L, Thatcher WW, Diaz T, Drost M, Wolfenson D. Effect of environmental heat stress on follicular development and steroidogenesis in lactating Holstein cows. Theriogenology 1993;39:797–810.
12. Bauman, D.E. and W.B. Currie, 1980. Partitioning of nutrients during pregnancy and lactation. A review of mechanisms involving homesostasis and homeorhesis. J. Dairy. Sci., 63: 1514.
13. Beede, D.K. and R.J. Collier, 1986. Potential nutritional strategies for intensively managed cattle during thermal stress. J. Anim. Sci., 62: 543-554.
14. Benjamin, M.M., 1981. Fluid and electrolytes. Outline of Veterinary Clinical Pathology. Iowa State Univ. Press, Ames. USA.
15. Bun C., Watanabe Y., Uenoyama Y., Inoue N., Ieda N., Matsuda F., Tsukamura H., Kuwahara M., Maeda K.I., Ohkura S., Pheng V. (2018). Evaluation of heat stress response in crossbred dairy cows under tropical climate by analysis of heart rate variability. J. Vet. Med. Sci., 80: 181–185.
16. Buttle, H.L., A.T. Cowie, E.A. Jones and A. Turvey, 1979. Mammary growth during pregnancy in hypophysectomized or bromocriptine-treated goats. J. Endocr., 80: 343-351.
17. Cardot V., Le Roux Y., Jurjanz S. (2008). Drinking behavior of lactating dairy cows and prediction of their water intake. J. Dairy Sci., 91: 2257–2264.
18. Chaiyabutr N., Chanpongsang S., Suadsong S. (2008). Effects of evaporative cooling on the regulation of body water and milk production in crossbred Holstein cattle in a tropical environment. Int. J. Biometerol., 52: 575–585.
19. Collier R.J., Dahl G.E., VanBaale M.J. (2006). Major advances associated with environmental effects on dairy cattle. J. Dairy Sci., 89: 1244–1253.
20. Collier R.J., Gebremedhin K., Macko A.R., Roy K.S. (2012). Genes involved in the thermal tolerance of livestock. In: Environmental stress and amelioration in livestock production, Sejian V., Naqvi S.M.K., Ezeji T., Lakritz J., Lal R. (eds). Springer-Verlag (publisher), Berlin Heidelberg, Germany, pp. 379–410.
21. Chebel, R. C., J. E. P. Santos, J. P. Reynolds, R. L. A. Cerri, S. O. Juchem, and M. Overton. 2004. Factors affecting conception rate after artificial insemination and pregnancy loss in lactating dairy cows. Anim. Reprod. Sci. 84:239–255. https://doi.org/10.1016/j .anireprosci.2003.12.012.
22. Chowers, I., H.T. Hammel, J. Eisenman, R.M. Abrams and S.M. McCann, 1966. Comparison of effect of environmental and preoptic heating and pyrogen on plasma cortisol. Amer. J. Physiol., 210: 606.
23. Collier, R. J., R. M. Eley, A. K. Sharma, R. M. Pereira, and D. E. Buffington. 1981. Shade management in subtropical environment for milk yield and composition in Holstein and Jersey cows. J. Dairy Sci. 64:844–849. https://doi.org/10.3168/jds.s0022-0302(81)82656 -2.
24. Collier, R.J., D.K. Beede, W.W. Thatcher, L.A. Israel and C.J. Wilcox, 1982. Influences of environment and its modification on dairy animal health and production. J. Dairy Sci., 65: 2213-2227.
25. Cunningham, J.G. and B.G. Klein, 2007. Veterinary Physiology. (4 .Ed.) Saunders Elsevier. Missouri. th USA.
26. Dalcin V.C., Fischer V., Daltro D.D., Alfonzo E.P., Stumpf M.T., Kolling G.J., Sil-va M.V., McManus C. (2016). Physiological parameters for thermal stress in dairy cattle. R. Bras. Zootec., 45: 458–465
27. Da Silva R.G., Guilhermino M.M., Morais D.A.E.F. (2010). Thermal radiation absorbed by dairy cows in pasture. Int. J. Biometeorol., 54: 5–11.
28. Davis S., Mader T. (2003). Adjustments for wind speed and solar radiation to the temperaturehumidity index. Nebr. Beef. Cattle Rep., 224: 48–51.
29. De Rensis, F., and R. J. Scaramuzzi. 2003. Heat stress and seasonal effects on reproduction in the dairy cow—A review. Theriogenology 60:1139–1151. https://doi.org/10.1016/s0093-691x(03)00126-2.
30. Dikmen, S., and P. J. Hansen. 2009. Is the temperature-humidity index the best indicator of heat stress in lactating dairy cows in a subtropical environment? J. Dairy Sci. 92:109–116. https://doi .org/10.3168/jds.2008-1370.
31. Eigenberg R.A., Brown - Brandl T.M., Nienaber J.A., Hahn G.L. (2005). Dynamic response indicators of heat stress in shaded and non-shaded feedlot cattle, Part 2: Predictive Relationships. Biosyst. Eng., 91: 111–118
32. Ealy AD, Drost M, Robinson OW, Britt JH. Developmental changes in embryonic resistance to adverse effects of maternal heat stress in cows. J Dairy Sci 1993;76:2899–905.
33. Ellis, W.C., J.H. Matis, K.R. Pond, C.E. Lascano and J.P. Telford, 1984. Dietary influences on flow rate and digestive capacity. In: F.M.C. Gilchrist and R. I. Mackie (Ed.) Herbivore Nutrition in the Subtropics and Tropics. pp.269-293. The Science Press (PTY) Ltd., Craighill, South Africa.
34. El-Nouty, F.D., I.M. Elbanna, T.P. Davis and H.D. Johnson, 1980. Aldosterone and ADH response to heat and dehydration in cattle. J. Appl. Physiol. Respir. Environ. Exercise Physiol., 48: 249.
35. Engelhardt, W. Von and J.R.S. Hales, 1977. Partition of capillary blood flow in rumen, reticulum and omasum of sheep. Amer. J. Physiol., 232: E53.
36. Fong, B. Y., Norris, C. S. & MacGibbon, A. K. H. Protein and lipid composition of bovine milk-fat-globule membrane. International Dairy Journal 17, 275–288 (2007).
37. Godyń D., Herbut E., Walczak J. (2013). Infrared thermography as a method for evaluating the welfare of animals subjected to invasive procedures – a review. Ann. Anim. Sci., 13: 423–434.
38. González Pereyra A.V., Maldonado May V., Catracchia C.G., Herrero M.A., Flores M.C., Mazzini M. (2010). Influence of water temperature and heat stress on drinking water intake in dairy cows. Chil. J. Agric. Res., 70: 328–336.
39. Gauthier D. The influence of season and shade on estrous behaviour, timing of preovulatory LH surge and the pattern of progesterone secretion in FFPN and Creole heifers in a tropical climate. Reprod Nutr Dev 1986;26:767–75.
40. Gilad E, Meidan R, Berman A, Graber Y, Wolfenson D. Effect of heat stress on tonic and GnRH-induced gonadotrophin secretion in relation to concentration of oestradiol in plasma of cyclic cows. J Reprod Fertil 1993;99:315–21.
41. Gröhn, Y. T., D. J. Wilson, R. N. González, J. A. Hertl, H.

Schulte, G. Bennett, and Y. H. Schukken. 2004. Effect of pathogen-specific clinical mastitis on milk yield in dairy cows. J. Dairy Sci. 87:3358– 3374. https://doi.org/10.3168/jds.s0022-0302(04)73472-4.

42. Gwazdauskas FC, Thatcher WW, Kiddy CA, Pape MJ, Wilcox CJ. Hormonal pattern during heat stress following PGF2alpha-tham salt induced luteal regression in heifers. Theriogenology 1981;16:271–85.
43. Gwazdauskas FC, Wilcox CJ, Thatcher WW. Environmental and management factors affecting conception rate in a subtropical climate. J Dairy Sci 1975;58:88–92.
44. Hammami H., Bormann J., M'Hamdi N., Montaldo H.H., Gengler N. (2013). Evaluation of heat stress effects on production traits and somatic cell score of Holsteins in a temperate environment. J. Dairy Sci., 96: 1844–1855.
45. Hempel S., König M., Menz C., Janke D., Amon B., Banhazi T.M., Estellés F., Amon T. (2018). Uncertainty in the measurement of indoor temperature and humidity in naturally ventilated dairy buildings as influenced by measurement technique and data variability. Biosyst. Eng., 166: 58–75.
46. Herbut P., Angrecka S., Godyń D. (2018 a). Effect of the duration of high air temperature on cow's milking performance in moderate climate conditions. Ann. Anim. Sci., 18: 195–207.
47. Herbut P., Angrecka S., Nawalany G. (2013). Influence of wind on air movement in a free stall barn during the summer period. Ann. Anim. Sci., 13: 109–119.
48. Herbut P., Angrecka S., Walczak J. (2018 b). Environmental parameters to assessing of heat stress in dairy cattle – a review. Int. J. Biometerol., 62: 2089–2097
49. Hill D.L., Wall E. (2015). Dairy cattle in a temperate climate: the effects of weather on milk yield and composition depend on management. Animal, 9: 138–149.
50. Hoffmann G., Schmidt M., Ammon C., Rose - Meierhöfer S., Burfeind O., Heu - wieser W., Berg W. (2013). Monitoring the body temperature of cows and calves using video recordings from an infrared thermography camera. Vet. Res. Commun., 37: 91–99.
51. Hammami, H. et al. Genetic analysis of heat stress effects on yield traits, udder health, and fatty acids of Walloon Holstein cows. J Dairy Sci 98, 4956–68 (2015)
52. Hansen, P. J., and C. F. Aréchiga. 1999. Strategies for managing reproduction in the heat-stressed dairy cow. J. Anim. Sci. 77:36. https://doi.org/10.2527/1997.77suppl_236x.
53. Howell JL, Fuquay JW, Smith AE. Corpus luteum growth and function in lactating Holstein cows during spring and summer. J Dairy Sci 1994;77:735–9.
54. Hu, H., Y. Zhang, N. Zheng, J. Cheng, and J. Wang. 2016. The effect of heat stress on gene expression and synthesis of heat-shock and milk proteins in bovine mammary epithelial cells. Anim. Sci. J. 87:84–91. https://doi.org/10.1111/asj.12375.
55. Igono, M.O., H.D. Johnson, B.J. Steevens, W.A. Hainen and M.D. Shanklin, 1988. Effect of season on milk temperature, milk growth hormone, prolactin and somatic cell counts of lactating cattle. Intl. J. Biometeor., 32: 194-200.
56. Ingraham RH, Gillette DD, Wagner WD. Relationship of temperature and humidity to conception rate of Holstein cows in subtropical climate. J Dairy Sci 1974;57:476–81.
57. Johnson J.M., Proppe D.W. (1996). Cardiovascular adjustments to heat stress. In: Handbook of physiology: Environmental physiology, Fregly M.J., Blatteis C.M. (eds). Oxford University Press, New York, USA, pp. 215–243.
58. Jensen, R. G. The composition of bovine milk lipids: January 1995 to December 2000. J Dairy Sci 85, 295–350 (2002).
59. Johnson, H.D., P.S. Katti, L. Hahn and M.D. Shanklin, 1988. Short-term heat acclimation effects on hormonal profile of lactating cows. Univ. of Missouri Rsch. Bull. No. 1061. Columbia. USA.
60. Kadzere C.T., Murphy M.R., Silanikove N., Maltz E. (2002). Heat stress in lactating dairy cows: a review. Livest. Prod. Sci., 77: 59–91.
61. Kovács L., Kézér F.L., Ruff F., Jurkovich V., Szenci O. (2018). Assessment of heat stress in 7-week old dairy calves with non-invasive physiological parameters in different thermal environments. Plos One, 13: e0200622.
62. Lambertz C., Sanker C., Gauly M. (2014). Climatic effects on milk production traits and somatic cell score in lactating Holstein-Friesian cows in different housing systems. J. Dairy. Sci., 97: 319–329.
63. Lees A.M., Lees J.C., Lisle A.T., Sullivan M.L., Gaughan J.B. (2018). Effect of heat stress on rumen temperature of three breeds of cattle. Int. J. Biometeorol., 62: 207–215.
64. Lemerle C., Goddard M.E. (1986). Assessment of heat stress in dairy cattle in Papua New Guinea. Trop. Anim. Health Prod., 18: 232–242.
65. Lacetera, N., Bernabucci, U., Ronchi, B. & Nardone, A. Physiological and productive consequences of heat stress: the case of dairy ruminants. In Interactions between climate and animal production (eds. Lacetera, N. et al.) 45–59 (Wageningen Academic Publishers, 2003).
66. Lee CN. Environmental stress effect on bovine reproduction. Vet Clin North Am 1993;9:263–73.
67. Lindner, H.R., 1964. Comparative aspects of cortisol transport. Lack of firm binding to plasma proteins in domestic ruminants. J. Endocrinol., 28: 301.
68. Linvill, D. E., and F. E. Pardue. 1992. Heat stress and milk production in the South Carolina coastal plains. J. Dairy Sci. 75:2598–2604. https://doi.org/10.3168/jds.s0022-0302(92)78022-9.
69. Lippke, H., 1975. Digestibility and volatile fatty acids in steers and wethers at 21 and 32 C ambient temperatures. J, Dairy Sci., 58: 1860.
70. Lippsett, M.B., T.L. Schwartz and N.A. Thon, 1961. Hormonal control of sodium, potassium, chloride and water metabolism. In: Comar, C.L. and F. bonner (Ed.) Mineral Metabolism, Vol. lB. Academic Press, New York. USA.
71. Madan ML, Johnson HD. Environmental heat effects on bovine luteinizing hormone. J Dairy Sci 1973;56:1420–3.
72. Magdub, A., H.D. Johnson and R.L. Belvea, 1982. Effect of environmental heat and dietary fiber on thyroid physiology of lactating cows. J. Dairy. Sci., 65: 2323.
73. Mansson, H. L. Fatty acids in bovine milk fat. Food Nutr Res 52 (2008)
74. McGuire, M.A., D.K. Beede, M.A. DeLorenzo, C.J. Wilcox, G.B. Huntington, C.K. Reynolds and R.J. Collier, 1989. Effects of thermal stress and level of feed intake on portal plasma flow and net fluxes of metabolites in lactating Holstein cows. J. Anim. Sci., 67: 1050-1060.
75. Mihm M, Baguisi A, Boland MO, Roche JF. Association between the duration of dominance of the ovulatory follicle and pregnancy rate in beef heifers. J Reprod Fertil 1994;102:123–30.
76. Mitra, R., G.I. Christison and H.D. Johnson, 1972. Effect of prolonged thermal exposure on growth hormone (GH) secretion in cattle. J. Anim. Sci., 34: 776-779.
77. Noordhuizen J., Bonnefoy J.M. (2015). Heat stress in dairy cattle: major effects and practical management measures for prevention and control. SOJ Vet. Sci., 1: 1–7. Doi: http://dx.doi.org/10.15226/2381-2907/1/1/00103.
78. NRC. 2001. Nutrient Requirements of Dairy Cattle. 7th rev. ed. Natl. Acad. Sci., Washington, DC.
79. Orihuela, A. 2000. Some factors affecting the behavioral manifestation of oestrus in cattle: A review. Appl. Anim. Behav. Sci. 70:1–16. https://doi.org/10.1016/s0168-1591(00)00139-8
80. Palmquist, D. L. Milk Fat: Origin of Fatty Acids and Influence of Nutritional Factors Thereon. In Advanced Dairy Chemistry Volume 2 Lipids (eds Fox, P. F. & McSweeney, P. L. H.) 43–92 (Springer US, Boston, MA, 2006).
81. Palta P, Mondal S, Prakas BS, Madan ML. Peripheral inhibin levels in relation to climatic variations and stage of estrous cycle in buffalo (Bubalus bubalis). Theriogenology 1997;47:898–995
82. Pereira, M. H. C., A. D. P. Rodrigues, T. Martins, W. V. C. Oliveira, P. S. A. Silveira, M. C. Wiltbank, and J. L. M. Vasconcelos. 2013. Timed artificial insemination programs during the summer in lactating dairy cows: Comparison of the 5-d Cosynch protocol with an estrogen/progesterone-based protocol. J. Dairy Sci. 96:6904– 6914. https://doi.org/10.3168/jds.2012-6260
83. Purwanto, B. P., Y. Abo, R. Sakamoto, F. Furumoto, and S. Yamamoto. 1990. Diurnal patterns of heat production and

heart rate under thermoneutral conditions in Holstein Friesian cows differing in milk production. J. Agric. Sci. 114:139 https://doi.org/10.1017/ s0021859600072117.

84. Putney DJ, Mullins S, Thatcher WW, Drost M, Gross TS. Embryonic development in superovulated dairy cattle exposed to elevated ambient temperature between the onset of estrus and insemination. Anim Reprod Sci 1989;19:37–51.
85. Ray DE, Halbach TJ, Armstrong DV. Season and lactation number effects on milk production and reproduction in dairy cattle in Arizona. J Dairy Sci 1992;75:2976–83.
86. Renaudeau, D., A. Collin, S. Yahav, V. De Basilio, J. L. Gourdine, and R. J. Collier. 2012. Adaptation to hot climate and strategies to alleviate heat stress in livestock production. Animal 6:707–728. https://doi.org/10.1017/s1751731111002448.
87. Rhoads, M. L., R. P. Rhoads, M. J. VanBaale, R. J. Collier, S. R. Sanders, W. J. Weber, B. A. Crooker, and L. H. Baumgard. 2009. Effects of heat stress and plane of nutrition on lactating Holstein cows: I. Production, metabolism, and aspects of circulating somatotropin. J. Dairy Sci. 92:1986–1997. https://doi.org/10.3168/ jds.2008-1641.
88. Rivera RM, Hansen PJ. Development of cultured bovine embryos after exposure to high temperatures in the physiological range. Reproduction 2001;121:107–15.
89. Roman-Ponce H, Thatcher WW, Canton D, Barron DH, Wilcox CJ. Thermal stress effects on uterine blood flow in dairy cows. J Anim Sci 1978;46:175–80.
90. Roman-Ponce H, Thatcher WW, Wilcox CJ. Hormonal interrelationship and physiological responses of lactating dairy cows to shade management system in a subtropical environment. Theriogenology 1981;16:139–54.
91. Rosemberg M, Folman Y, Herz Z, Flamenbaum I, Berman A, Kaim M. Effect of climatic condition on peripheral concentrations of LH, progesterone and oestradio-17beta in high milk-yielding cows. J Reprod Fertil 1982;66:139–46.
92. Roth Z, Meidan R, Braw-Tal R, Wolfenson D. Immediate and delayed effect of heat stress on follicular development and its association with plasma FSH and inhibin concentration in cows. J Reprod Fertil 2000;120:83–90.
93. Roth, Z., A. Arav, A. Bor, Y. Zeron, R. Braw-Tal, and D. Wolfenson. 2001. Improvement of quality of oocytes collected in the autumn by enhanced removal of impaired follicles from previously heat-stressed cows. Reproduction 122:737–744. https://doi.org/10 .1530/rep.0.1220737.
94. Rushen, J., L. Munksgaard, P. G. Marnet, and A. M. De Passillé. 2001. Human contact and the effects of acute stress on cows at milking. Appl. Anim. Behav. Sci. 73:1–14. https://doi.org/10.1016/s0168 -1591(01)00105-8.
95. Rutledge JJ, Monson RL, Northey DL, Leibfried-Rutledge ML. Seasonality of cattle embryo production in a temperate region. Theriogenology 1999;51:330 [abstract].
96. Ryan DP, Boland MP. Frequency of twin births among Holstein X Friesian cows in a warm dry climate. Theriogenology 1991;36:1–10.
97. Schutz K.E, Rogers A.R., Cox N.R., Tucker C.B. (2009). Dairy cows prefer shade that offers greater protection against solar radiation in summer: Shade use, behaviour, and body temperature. Appl. Anim. Behav. Sci., 116: 28–34.
98. Schutz K.E., Cox N.R., Mattews L.R. (2008). How important is shade to dairy cattle? Choice between shade or lying following different levels of lying deprivation. Appl. Anim. Behav. Sci., 114: 307–318.
99. Slimen B.I., Taha N., Abdeljelil G., Manef A. (2016). Heat stress effects on livestock: molecular, cellular and metabolic aspects, a review. J. Anim. Physiol. Anim. Nutr., 100: 401–412.
100. Stevens D.C. (1981). A model of respiratory vapor loss in Holstein dairy cattle. Trans ASAE, 24: 151–153.
101. Sánchez-Juanes, F., Alonso, J. M., Zancada, L. & Hueso, P. Distribution and fatty acid content of phospholipids from bovine milk and bovine milk fat globule membranes. International Dairy Journal 19, 273–278 (2009).
102. Schär, C., P. L. Vidale, D. Lüthi, C. Frei, C. Häberli, M. A. Liniger, and C. Appenzeller. 2004. The role of increasing temperature variability in European summer heatwaves. Nature 427:332–336. https://doi.org/10.1038/nature02300.
103. Schüller, L. K., O. Burfeind, and W. Heuwieser. 2014. Impact of heat stress on conception rate of dairy cows in the moderate climate considering different temperature–humidity index thresholds, periods relative to breeding, and heat load indices. Theriogenology 81:1050–1057. https://doi.org/10.1016/j.theriogenology.2014.01 .029.
104. Silanikove, N., 2000. Effects of heat stress on the welfare of extensively managed domestic ruminants. Livestock Production Science, 67: 1-18.
105. Spiers, D. E., J. N. Spain, J. D. Sampson, and R. P. Rhoads. 2004. Use of physiological parameters to predict milk yield and feed intake in heat-stressed dairy cows. J. Therm. Biol. 29:759–764. https://doi .org/10.1016/j.jtherbio.2004.08.051.
106. Taylor N.A., Tipton M.J., Kenny G.P. (2014). Considerations for the measurement of core, skin and mean body temperatures. J. Therm. Biol., 46: 72–101.
107. Tucker C.B., Rogers A.R., Schutz K.E. (2008). Effect of solar radiation on dairy cattle behaviour, use of shade and body temperature in a pasture-based system. App. Anim. Behav. Sci., 109: 141–154.
108. Unruh E.M., Theurer M.E., White B.J., Larson R.L., Drouillard J.S., Schrag N. (2017). Evaluation of infrared thermography as a diagnostic tool to predict heat stress events in feedlot cattle. Am. J. Vet. Res., 78: 771–777.
109. Vasconcelos JLM, Silcox RW, Lacerda JA, Pursley GR, Wiltbank MC. Pregnancy rate, pregnancy loss, and response to heat stress after AI at 2 different times from ovulation in dairy cows. Biol Reprod 1998;56(Suppl 1):140 [abstract].
110. von Keyserlingk, M. A. G., and M. J. Hötzel. 2015. The ticking clock: Addressing farm animal welfare in emerging countries. J. Agric. Environ. Ethics 28:179–195.
111. von Keyserlingk, M. A. G., J. Rushen, A. M. de Passillé, and D. M. Weary. 2009. Invited review: The welfare of dairy cattle—Key concepts and the role of science. J. Dairy Sci. 92:4101–4111. https:// doi.org/10.3168/jds.2012-6354.
112. Wilson T.E., Crandall C.G. (2011). Effect of thermal stress on cardiac function. Exerc. Sport Sci. Rev., 39: 12–17.
113. Werner J., Mekjavic I.B., Taylor N.A.S. (2008). Concepts in physiological regulation: a thermoregulatory perspective. In: Physiological bases of human performance during work and exercise, Taylor N.A.S., Groeller H. (eds). Churchill Livingstone, London, United Kingdom, pp. 325–340.
114. West, J. W. 2003. Effects of heat-stress on production in dairy cattle. J. Dairy Sci. 86:2131–2144. https://doi.org/10.3168/ jds.s0022 -0302(03)73803-x.
115. Westwood, C. T., I. J. Lean, and J. K. Garvin. 2002. Factors influencing fertility of Holstein dairy cows: a multivariate description. J. Dairy Sci. 85:3225–3237. https://doi.org/10.3168/jds.s0022 -0302(02)74411-1.
116. Wetteman, R.P. and H.A. Tucker, 1979. Relationship of ambient temperature to serum prolactin in heifers. Proc. Soc. Exp. Biol. Med., 146: 909-911.
117. White, F. J., R. P. Wettemann, M. L. Looper, T. M. Prado, and G. L. Morgan. 2002. Seasonal effects on estrous behavior and time of ovulation in nonlactating beef cows. J. Anim. Sci. 80:3053–3059. https://doi.org/10.2527/2002.80123053x.
118. Wilde, C.J. and W.L. Hurley, 1996. Animal models for the study of milk secretion. J. Mammary Gland Biol. Neoplasia, 1: 123-134.
119. Wilson SJ, Marion RS, Spain JN, Spiers DE, Keisler DH, Lucy MC. Effect of controlled heat stress on ovarian function in dairy cattle: I. Lactating cows. J Dairy Sci 1998;1:2124–31.
120. Wise ME, Armstrong DV, Huber JT, Hunter R, Wiersma F. Hormonal alterations in the lactating dairy cow in response to thermal stress. J Dairy Sci 1988;71:2480–5.
121. Wolfenson D, Thatcher WW, Badinga L, Savio JD, Meidan R, Lew BJ, et al. The effect of heat stress on follicular development during the estrous cycle dairy cattle. Biol Reprod 1995;52:1106–13.
122. Yousef, M.K. and Johnson, H.D. 1966a. Blood thyroxine degradation rate in cattle as influenced by temperature and feed intake. Life Sci., 5: 1349.

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