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Respuestas de adaptación al estrés térmico en mamíferos

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Adaptive Responses to Thermal Stress in Mammals

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Abstract

The environment animals have to cope with is a combination of natural factors such as temperature. Extreme changes in these factors can alter homeostasis, which can lead to thermal stress. This stress can be due to either high temperatures or low temperatures. Energy transference for thermoregulation in homoeothermic animals occurs through several mechanisms: conduction, convection, radiation and evaporation. When animals are subjected to thermal stress, physiological mechanisms are activated which may include endocrine, neuroendocrine and behavioral responses. Activation of the neuroendocrine system affects the secretion of hormones and neurotransmitters which act collectively as response mechanisms that allow them to adapt to stress. Mechanisms which have developed through evolution to allow animals to adapt to high environmental temperatures and to achieve thermo tolerance include physiological and physical changes in order to reduce food intake and metabolic heat production, to increase surface area of skin to dissipate heat, to increase blood flow to take heat from the body core to the skin and extremities to dissipate the heat, to increase numbers and activity of sweat glands, panting, water intake and color adaptation of integument system to reflect heat. Chronic exposure to thermal stress can cause disease, reduce growth, decrease productive and reproductive performance and, in extreme cases, lead to death. This paper aims to briefly explain the physical and physiological responses of mammals to thermal stress, like a tool for biological environment adaptation, emphasizing knowledge gaps and offering some recommendations to stress control for the animal production system.

Keywords: hyperthermia, hypothermia, mammals, thermal shock.

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Respuestas de adaptación al estrés térmico en mamíferos

Resumen

El ambiente al que los animales tienen que enfrentarse es una combinación de factores naturales. Cambios extremos en estos factores pueden alterar la homeostasis y conducir al estrés térmico. Este puede resultar tanto de temperaturas altas como de temperaturas bajas. Cuando se somete a los animales a estrés térmico, se activan mecanismos fisiológicos que pueden incluir respuestas endocrinas, neuroendocrinas y de comportamiento. Los mecanismos desarrollados a través de la evolución para que los animales se adapten a temperaturas ambientales altas y alcancen termotolerancia incluyen cambios fisiológicos y físicos, a fin de reducir la ingesta de alimentos y la producción del calor metabólico; de aumentar el área superficial de la piel para disipar el calor; de aumentar el flujo de sangre para llevar el calor del núcleo del cuerpo a la piel y las extremidades para disipar el calor, o de aumentar el número y la actividad de las glándulas sudoríparas, el jadeo, la ingesta de agua y la adaptación del color del sistema de tegumento para reflejar el calor. La exposición crónica al estrés térmico puede causar enfermedad, reducir el crecimiento, disminuir el rendimiento productivo y reproductivo y, en casos extremos, llevar a la muerte. El objetivo de este trabajo es explicar las respuestas físicas y fisiológicas de los mamíferos al estrés térmico, como una herramienta para la adaptación al entorno biológico, haciendo hincapié en las lagunas de nuestro conocimiento y ofreciendo algunas recomendaciones para controlar el estrés en el sistema de producción animal.

Palabras clave: hipertermia, hipotermia, mamíferos, choque térmico.

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Respostas de adaptação ao estresse térmico em mamíferos

Resumo

O ambiente ao que os animais têm que enfrentar-se é uma combinação de fatores naturais. Mudanças extremas nestes fatores podem alterar a homeostase e levar ao estresse térmico. Este pode resultar tanto de temperaturas altas quanto de temperaturas baixas. Quando se submete os animais a estresse térmico, se ativam mecanismos fisiológicos que podem incluir respostas endócrinas, neuroendócrinas e de comportamento. Os mecanismos desenvolvidos através da evolução para que os animais se adaptem a temperaturas ambientais altas e alcancem termo tolerância incluem mudanças fisiológicas e físicas, visando reduzir a ingesta de alimentos e a produção do calor metabólico; de aumentar a área superficial da pele para dissipar o calor; de aumentar o fluxo de sangue para levar o calor do núcleo do corpo à pele e às extremidades para dissipar o calor, ou de aumentar o número e a atividade das glândulas sudoríparas, o arquejo, a ingestão de água e a adaptação da cor do sistema de tegumento para refletir o calor. A exposição crônica ao estresse térmico pode causar doença, reduzir o crescimento, diminuir o rendimento produtivo e reprodutivo e, em casos extremos, levar à morte. O objetivo deste trabalho é explicar as respostas físicas e fisiológicas dos mamíferos ao estresse térmico, como uma ferramenta para a adaptação ao entorno biológico, enfatizando nas lagoas de nosso conhecimento e oferecendo algumas recomendações para controlar o estresse no sistema de produção animal.

Palavras chave: hipertermia, hipotermia, mamíferos, choque térmico.

Introduction

Extreme ambient conditions can negatively affect animal production. Temperature, humidity, ventilation, pluviosity and light are related to the regulation of metabolic processes in animals, affecting the ability of the individual to adapt to its environment (1,2). In this way, many productive and reproductive parameters can be compromised, like nutrient intake, weight gain, milk production and fertility (3-5).

Heat stress affects quality of oocytes ovulated even when cows are subjected to high ambient temperatures from onset of estrus to time of ovulation (about 30 hours). Adaptive processes to mitigate heat stress begin at conception and continue throughout gestation. The objective of adaptation in this period is to achieve a successful outcome of gestation, survival of the neonate and lactation to nourish the offspring. In the neonatal period, adaptive challenges are greater because animals depend on their physiological responses controlled by their autonomic nervous system to cope with the new environment. In domestic animals, man plays an important role in the survival of the offspring, while survival of wild animals depends solely on the adaptive responses of the animal to its environment (1,6,7).

A determinant ambient factor is temperature. Homoeothermic animals have a *thermo-neutral zone* which is the range of ambient temperatures in which animals require minimal energetic expenses that do not compromise body reserves to maintain a constant body temperature (basal metabolic rate). This zone is specific for each species, but varies among breeds and genetic lines (1,2).

Another factor is the *thermal comfort zone*. Unlike in humans in which the concept is very subjective ("condition of mind in which it expresses satisfaction with the ambient temperature") (8), in animals the concept is well defined as the range of temperature and relative humidity

in which an animal is comfortable and its metabolic and physiologic processes are stable and directed to storage of carbohydrate, proteins and fat (2,9,10).

There are several indices to predict with some precision whether the environment is a potential heat stress factor for the animal. The most useful factors are shown in Table 1.

Table 1. Indices of thermal stress

Index	Variables	Scale
Temperature-Humidity Index (THI)	Temperature Humidity	<70 It is not stress 71 - 78 Critic 79 - 83 Danger indicator >83 Emergency
Black-Globe Humidity Index (BGHI)	Temperature Humidity Radiation	It should be evaluated based on the kind of animal and environment
Equivalent Temperature Index (ETI)	Temperature (C°) Humidity Wind Velocity	18-27 Comfort 28-32 Precaution 33-38 Extreme Precaution 39-44 Danger >44 Extreme Danger

Source: 11, 12, 13.

Temperature-Humidity Index (THI)

Conceived at the beginning as an indicator of thermic comfort in humans, later it was shown to be useful for animals of production as well. However, some researches, like Silva and collaborators, did not find any correlation between THI, temperature and respiratory rate, whereby it is possible that under some environmental conditions, like in the neotropics, this index might not be useful (11).

Black-Globe Humidity Index (BGHI)

The BGHI temperature and humidity index also takes into account radiation, being more useful when people are evaluating thermic stress in grazing animals that are in tropical regions (11-13).

Equivalent Temperature Index (ETI)

This index combines temperature, humidity and wind velocity (14). ETI shows representative results to heat exposition in short time periods, common in summer season in some warm regions. However, Silva and collaborators in a study on Holstein and Jersey cows in an equatorial region showed that ETI is one of the best indexes for tropical conditions, because it has significant correlations with corporal temperature and respiratory rate (11).

Silva and collaborators suggested in 2007 that it is important to consider not only temperature and humidity, but also thermic radiation and airflows, to make thermic stress indices suitable to environmental conditions and the kind of animal they are evaluating. For the evaluation of open air environment, in the case of grazing animals, it should seem that all of the variables are possible, both in environment and in physiological variables. In fact, the animal performance is the combination result of most of those variables. Some of those variables are complex and can change with time.

Temperature values out of the thermo-neutral range zone are defined as *superior critical temperature* and *inferior critical temperature*. In these temperatures homoeothermic animals have to adjust their metabolism to regulate their body temperature (15). When early adaptive responses do not compensate for changes in temperature, animals could be affected by thermal stress, also called caloric stress. Thermal stress is the activation process of physiological mechanisms in order to respond to thermogenic and thermolytic events. These responses are known as physiological responses to stress and they involve the activation of neuroendocrine pathways. If those responses are sustained for extended periods of time (chronic stress), the animals' production trait variables can be affected, causing a decrease in the efficiency of the production systems such as milk production, rate of growth and level of physical activity (1).

Physiological responses to thermal stress in animals include the activation of endocrine, autonomic and central nervous systems, as well as cardiovascular mechanisms

for redistribution of blood flow. All of them act in a synergic way depending on the magnitude of the stressor factor and they respond to it by generating physiological mechanisms to suppress or decrease the threat of the adverse effects of thermal stress (16).

The objective of this review is to explain the physical and physiological responses of mammals to thermal stress, like biological environment adaptation strategy, identifying the weak points in our knowledge.

Thermo-Conduction Mechanisms

Thermal energy in animals is transferred across gradients, i.e. from high thermal energy to low thermal energy. When ambient temperature increases above the comfort zone, it is transferred to the animal. In response to this, there is an increase in body temperature. On the contrary, when ambient temperature decreases below the comfort zone, the animal will suffer from a loss of caloric energy due to shivering or other responses to maintain body temperature (1,17).

Several routes exist for the loss or gain of thermal energy in animals (figures 1 and 2): conduction, convection, radiation and evaporation.

Conduction. Conduction is the transfer of heat by direct contact between any surface and the animal. It is characterized by the generation of variations in kinetic energy in cold molecules caused by other molecules. When ambient temperature increases, animals have to cope with thermal discomfort, so they change their behavior by modifying the posture of their bodies to allow direct contact with cooler surfaces like floor or walls in order to transfer thermal energy from themselves to those surfaces; this dissipates heat and decreases body temperature.

*Convection***.** It is the transference of thermal energy by the movement of air or water. Air and water can absorb heat by the redistribution of their particles. In animals, convection is carried out between skin and air by evapotranspiration, also known as sweating or panting (18).

Radiation. It is the exchange of thermal energy between two objects or animals which are not in contact through the transference of electromagnetic waves. Exchange of heat by radiation between an animal and its environment is achieved in accordance to the Stefan-Boltzman law, which establishes that the capacity of a black body to gain thermal energy by radiation is proportional to the fourth power of its absolute superficial temperature (T^4 in Kelvin grades). An example of radiation is thermal energy reflected by the soil and gained by the animal (1,18).

Evaporation. Water has a high specific heat, so when it evaporates as sweat, animals experience a decrease in body thermal energy. This process is favored over convection (19).

In the process of caloric transference by evaporation of water molecules, each gram of water (sweat) absorbs 0.58 Kcal of free energy that remains as latent heat of vaporization and favors thermoregulation. It is the most effective process for thermoregulation when ambient temperature is near body temperature (1,17).

These ways of transference of thermal energy collaboratively participate in the context of environment-animal interaction to generate the thermal ambient of the animal at a given moment (figures 1 and 2). However, adaptive responses of the animal before thermal stress are very dynamic in nature, as it is explained above.

Surface area allows animals to dissipate or gain heat, and the greater the surface the greater the dissipation or gain in thermal energy. There are differences in adaptation of thermal conditions between children and adults. Smaller blood volumes in children compared with adults, even relative to body size, may limit the potential for heat transfer during heat exposure and may compromise exercise performance in the heat. Testosterone and prolactin are two hormones that differ in baseline levels between children and adults and may affect the function of sweat glands and the composition of sweat. These possible effects of testosterone and prolactin require further investigation (20).

Figure 1. This figure summarizes the main mechanisms of thermal energy transfer between an animal and its environment, when this exceeds the upper temperature comfort range. Additionally, the figure shows physiological mechanisms of response and overall effects on animals

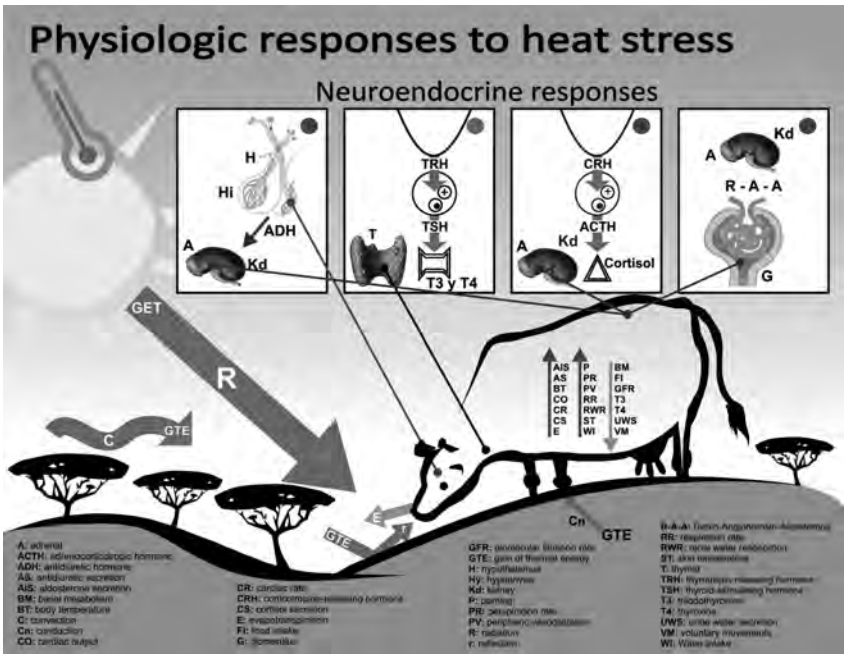
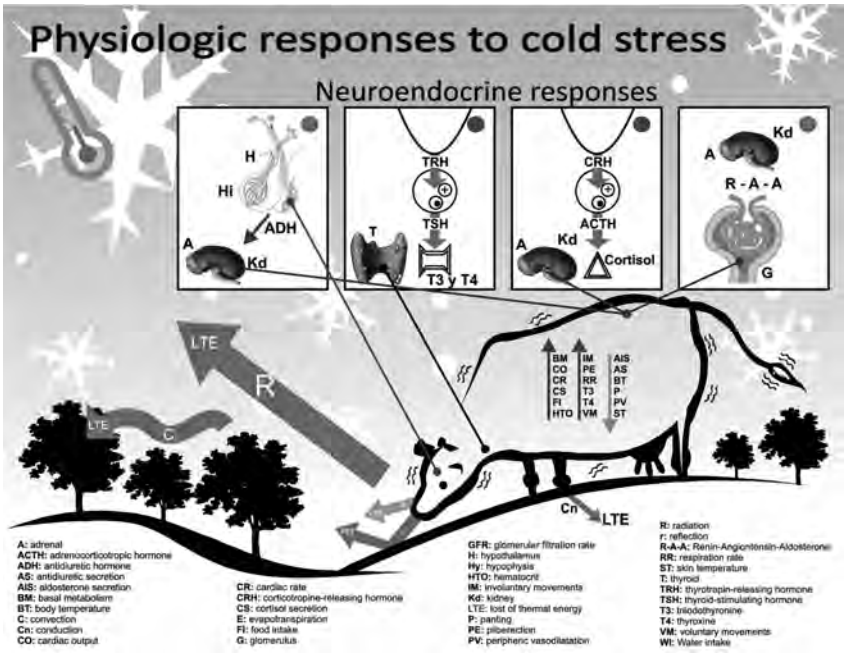


Figure 2. This figure shows the main mechanisms of thermal energy transfer between an animal and its environment, when this exceeds the lower temperature comfort range. Additionally, physiological mechanisms of response and overall effects on animals are summarized



Neuroendocrine Responses to Thermal Stress

Animals experience constant physiological changes in order to cope with diverse environmental situations (thermal, social and location), which can activate neuroendocrine responses. Stress leads to the activation of physiological mechanisms required to maintain homeostasis. Stress compromises important metabolic functions such as reproduction, immunity and growth (21,22).

Stress can be classified as acute or chronic depending on whether the exposure to drastic changes in temperature is for a short or a long period of time. Both activate neuroendocrine pathways that modify physiological processes in order to maintain homeostasis to ensure survival of the animal (23).

Stress hormones, produced in response to an increase in environmental temperature, induce the following effects in animals: Mobilization of energy for maintenance of muscular and neural functions; increase in the perception of the environment; increase in brain perfusion for delivery of glucose; improvements in cardiovascular and respiratory functions; modulation of immune responses; decrease in reproductive and sexual functions; and decrease in appetite (24).

Neuroendocrine responses in animals submitted to stress are diverse and include release and activation of several tropic hormones like adrenocorticotropic hormone (ACTH), thyrotrophic hormone (TSH), somatotropic or growth hormone (GH), follicle stimulating (FSH) and luteinizing (LH) hormones, and prolactin (PRL) (25). Some functions of these hormones will be discussed.

Hypothalamus-Hypophyseal-Adrenal axis (HHAa)

Hans Selye (26) was the first person to describe the neuroendocrine responses of the body to stress. He suggested that when individuals were submitted to stressful situations, they activated the sympathetic nervous system (SNS) and HHAa triggered the so-called "general adaptation syndrome" (5,19,25,27).

Activation of HHAa is initiated in the animal in response to changes in temperature that are outside of the thermal comfort zone of the species. Those changes are initially perceived by the peripheral nervous system and then assimilated by the central nervous system, wherein the paraventricular nucleus of the hypothalamus is stimulated to release corticotropin releasing hormone (CRH) (28). CRH is released into the hypothalamus-hypophyseal portal system to induct the synthesis and secretion of ACTH into the blood stream. ACTH stimulates the *zona fasciculata* of the adrenal cortex to synthesize and secrete cortisol into blood to exert its physiological actions in target tissues (muscle, liver and adipose tissue) (17,28,29).

Cortisol is a member of the steroid hormone family whose common precursor is cholesterol. Due to its low solubility in blood it is transported by special proteins (corticosteroid binding globulin [CBG]) to target tissues (17) and only 10% of cortisol is in free form. It has been demonstrated that animals submitted to stress (noise, physical perturbation or changes in ambient temperature) have an increase in circulating concentrations of CBG and free cortisol. This finding shows that the secretion of cortisol is one of the most important hormonal responses to stress (30).

The main physiologic effect of cortisol produced by a thermal stress is the mobilization of energy for the maintenance of muscular and neural functions. Cortisol directly influences metabolism and behavior in animals submitted to thermal stress. It affects glycogenolysis, lipolysis and proteolysis in order to provide the energy required to restore homeostasis (figures 1 and 2). High concentrations of cortisol in serum are associated with an increase in aggressive behavior in some animals (17,31).

Autonomic Nervous System (ANS)

ANS is part of the nervous system that regulates body processes related to expenditure and storage of energy.

ANS is anatomically organized into preganglionic and postganglionic neuronal nets and it is physiologically divided into sympathetic and parasympathetic nervous systems (32). The sympathetic nervous system responds to stressful situations.

The sympathetic nervous system presents short preganglionic axons, emerging from the thoracolumbar spinal cord, and long postganglionic axons (32,33). Synapses between these two types of axons are mediated by neurotransmitter acetylcholine (AC). Some effects of AC are to induce vasodilatation of blood vessels in skeletal muscle and to activate sweating (34). Synapses between postganglionic axons and target tissues are mediated by catecholamine, mainly neurotransmitter adrenaline, which induces the following effects: contraction of the spleen, tachycardia, hemodynamic modifications such as vasoconstriction of peripheral blood vessels, and decrease in gastrointestinal contractions (17,19,33). Liberation of adrenaline occurs in animals faced with acute stressful situations such as thermal changes and pain that lead to behavioral and physiological changes (32).

Thyroid Hormones

The thyroid gland produces triiodothyronine (T3) and tetraiodothyronine or thyroxine (T4) in response to stimulation by TSH produced by thyrotropic cells in the anterior hypophysis. Regulation of TSH is by thyroid releasing hormone (TRH). Both T3 and T4 are transported in serum by specific proteins due to their low solubility in blood. T4 is the precursor of T3, and T3 has the highest biological activity (35).

Thyroid hormones control cellular metabolism that favors oxygen consumption and energy generation needed for tissue activities. Oxygen consumption in cells is related to increase in mitochondrial activity and generation of heat. High levels of thyroid hormones increase cellular respiration, ATP generation, cellular growth, cardiac and respiratory rates and catabolic pathways (36,37).

In cases of thermal stress, secretion of releasing and tropic hormones is affected. When an animal is subjected to high ambient temperatures, secretion of those hormones is inhibited in order to avoid thermogenesis. On the other hand, when an animal is subjected to ambient cold, those hormones are released to promote catabolic pathways that favor body thermogenesis. In this case, secretion of T3 and T4 is stimulated (17). When stress is chronic, physiologic functions of T3 are decreased due to high levels of glucocorticoids that inhibit transformation of T4 in T3 (figures 1 and 2) (35).

Antidiuretic Hormone (ADH)

This is a hormone synthesized and secreted by supraoptic and paraventricular hypothalamic nuclei into the blood stream and transported to target tissues. It is also known as vasopressin due to its regulatory effect on blood pressure. ADH is a vital hormone for water homeostasis in a thermal stress event as its main function is to reabsorb water in the kidney. However, the pattern of ADH secretion varies in accordance with the type of thermal stress (22).

In heat stress, thermolytic routes are activated for sweating and cooling via evaporation. Constant liquid losses stimulate baroreceptors in the atrium and greater blood vessels, as well as hypothalamic osmoreceptors, which induce ADH release to prevent dehydration. There is an inhibition of ADH during cold stress which favors water loss by urination to avoid heat transference from tissues to water, generating polyuria (Figures 1 and 2) (22).

Renin-Angiotensin-Aldosterone System (RAA)

These hormones are related to the maintenance of homeostasis for electrolytes. RAA is activated when blood flow is reduced in the afferent arteriole of glomeruli of the kidney due to hypovolemia. Hypovolemia can result from dehydration as a consequence of high ambient heat. The decrease in blood flow to the kidney induces secretion of renin from the juxtaglomerular apparatus. Once renin is produced, it stimulates the synthesis and secretion of angiotensin, which induces the synthesis and secretion of aldosterone from the adrenal cortex (36).

Aldosterone stimulates reabsorption of water and ions, principally sodium, in the kidney in order to avoid massive excretion of water and to maintain blood pressure. In cold stress, sensitivity of the juxtaglomerular apparatus is inhibited, favoring water excretion (polyuria) (figures 1 and 2) (22,36,38).

Recent studies suggest that other hormones, like progesterone, insulin, oxytocin, androgens and estrogens, play a role in responses to thermal stress via undefined physiological mechanisms (5).

Body Responses to Heat and Cold Stress

Animals constantly interact with their environment. Thermoconduction is a process by which animals can lose or gain thermal energy based on fluctuations in ambient temperature (36).

Physiological responses to thermal stress in animals depend basically on the nature of the temperature change outside the thermal comfort zone (7,17).

Responses to Heat Stress

Water is approximately 65% of the body weight of an animal. Thus water is very important for thermoconduction and thermoregulation. Animals are frequently affected by high ambient temperatures, increasing body temperature if the loss of intrinsic heat does not exceed extrinsic heat gain. Once thermal homeostasis is lost, animals activate physiological mechanisms to reestablish a dynamic balance (7).

Peripheral vasodilatation of blood vessels. This is an increase in the body's total surface area of peripheral blood vessels to favor dissipation of thermal energy from an animal's body to its environment mediated via increased nitric oxide production (18,39).

Hemodynamic changes. Increase in cardiac output and blood flow to the skin optimizes caloric interchange with the environment (18,40).

Activation of neuroendocrine responses. The acute secretion of catecholamines and activation of HHAa, as well as a decrease in T3 secretion avoid the generation of more metabolic energy by an animal (35).

Stimulation of the thermoregulatory hypothalamic center. In order to initiate panting which allows evaporative cooling from the oral cavity.

Behavioral changes. Animals avoid direct exposure to radiation from the sun, for example, by occupying strategic places that favor thermoregulation (41). Furthermore, animals decrease food intake and physical activity to avoid metabolic thermogenesis (18,42). Canines extend their body in cold places in order to increase contact of their superficial surface, skin and hair, with soil and floor to conduct heat from the skin to the cooler soil or floor (43). Swine lump together to conserve temperature and avoid leakage of heat.

Increase in sweating. Increases in body temperature stimulate thermoreceptors that activate sweat glands (Figure 1) (35,39).

In the absence of sweating, heat stored in body core is not dissipated and may produce hyperthermia (44,45).

Numerous studies have identified that direct solar radiation on the body surface of animals affect not only productive but also welfare indicators. As an alternative to counteract these effects, some research has shown that the use of shading can reduce adverse thermal effects in animals (18).

Responses to Cold Stress

When environmental temperature decreases below the thermal comfort level, heat loss must equal endogenous heat production (thermogenesis) in order to achieve homeostasis, i.e. maintenance of body temperature in a stable thermo neutral range (46). Cold stress activates several physiological responses.

Peripheral vasoconstriction. Vasoconstriction of peripheral blood vessels decreases loss of thermal energy and con-

serves heat in vital organs to maintain an optimal body temperature (34). In extreme cold, there may be a transfer of heat from arteries to legs and arms to veins draining them to conserve heat in blood vessels.

Activation of neuroendocrine responses. Similar to heat stress, acute secretion of catecholamines and activation of HHAa result in an increase in T3 secretion in order to favor metabolic thermogenesis, i.e. concentrations of adrenaline, noradrenaline, β-endorphin and cortisol in plasma increase in response to exercise in cool dry conditions in horses (25,47).

Inhibition of thermoregulatory hypothalamic center. This minimizes heat loss by evapotranspiration (25).

Behavioral changes. To prevent leakage of heat, animals increase physical activity, food intake and promote gregarious behavior. However, these behavioral changes can occur according to age and metabolic demand. Growing horses reduce their feed intake while increase energy intake, adult horses adjust feed to prevent decreasing of core temperature by increasing energy intake, shivering and promoting behavioral changes (40).

Piloerection. Erection of hair on skin reduces loss of thermal energy by convection (Figure 2).

Muscular involuntary contractions or shivering. Contraction or twitching of muscles in cold, known as shivering, produces endogenous heat as a form of metabolic work (13,48).

Adaptive Mechanisms to Thermal Stress

Adaptation is a coordinated series of processes by which stressor agents are overcome, allowing the animal to efficiently cope with the internal and external environment. Every individual has to experience an exposure to the stressor agent to generate adaptive responses and maintain a dynamic balance in thermal homeostasis within the comfort zone (49).

There are two types of adaptation: genetic (GA) and physiological (PA). GA implies changes in gene expression or modifications in coding regions of genetic material and requires a high number of generations through evolution to adapt to heat or cold stress (50). On the other hand, PA implies modifications in physiological processes that are independent of changes in gene expression to achieve the adaptive response (46).

Physiological Adaptation to Cold

When an animal adapted to hot weather (38-40 ºC, 760 mmHg approx.) is brought to a place with cold weather (8-16 ºC, 420 mmHg approx.) without a previous and gradual exposure to that temperature, physiological hypoxia is presented. Oxygen particles in a low atmospheric pressure situation are more disperse, which leads to difficult breath and deleterious distribution of oxygen in tissues. In this way, hypoxia is the first stimulus to initiate physiological adaptation (51).

Tolerance to cold temperatures depends on adaptive characteristics such as longer, thicker and denser fur/hair, as well as an increase in distribution and quantity of body fat and in food intake (52-55).

As a result of chronic exposition to new ambient conditions, some variables increase respiratory rate to incorporate a higher volume of oxygen in each inhalation, cardiac frequency to improve oxygen distribution in tissues, and tissue perfusion to favor oxygen diffusion, constrict peripheral blood vessels to conserve thermal energy via actions of cytokines and prostaglandins (56).

Hypoxia is one of the more relevant physiological changes in response to cold stress. In response to hypoxia, organisms generate new red blood cells (polycythemia) which results in: (1) an increase in hematocrit to improve oxygen distribution in tissues; (2) an increase in cardiac size (cardiac hypertrophy) which improves cardiac output and the velocity of delivery of nutrients to tissues; (3) an increase in vasodilation of pulmonary vessels which favors absorption of oxygen; and (4) an increase

in vascularity and contractility of skeletal, cardiac and smooth muscle as well as mitochondrial function (56).

Physiological Adaptation to Heat

As body temperature increases when an animal is exposed to high ambient temperatures, peripheral and central receptors located in the preoptic area of the hypothalamus are activated. The hypothalamus is responsible for initiating efferent signals for vasodilatation of peripheral vessels and activation of sweat glands that allow the animal to dissipate heat from body surface. These are the primary responses that allow an animal to adapt to high ambient temperatures (57).

Physiological changes in response to chronic exposure to high ambient temperatures are increases in heart rate in beats per minute which increases blood flow to peripheral vessels to dissipate heat. There is an increase in respiratory rate to dissipate heat by evaporation, an increase in intake of water or other liquids to maintain a constant rate of sweating, and the activation of RAA system to avoid excessive loss of sodium and other electrolytes from blood. In general, the adaptation process can be attained within one week after the initiation of exposure to hot environment; however, this depends on multiple factors including air temperature and wind velocity, sanitary status, body condition, genetics of the animal and the presence of another stress factors such as poor nutrition and lack of water (figures 1 and 2) (57).

Some species have developed anatomic-physiological adaptations to optimize heat loss, prioritizing vital organs. The horse, a species without a carotid rete (that exist in other animals), can selectively cool the brain during exercise or heat exposure. This occurs, at least in part, via presence of cool blood within the cavernous sinus, presumably resulting principally from the cooling of venous blood within the upper respiratory tract (58).

One of the major factors affecting the ability of an individual to efficiently adapt to hot environments is the relative humidity of the environment. Previous studies were able to determine that in animals subjected to hot spots with high relative humidity the risk of dying considerably increases, due to the physiological responses triggered (59).

Evolutionary Adaptations to Thermal Stress

During the evolution of different breeds within a species, adaptive mechanisms have been developed in response to climatic conditions in which the species/breed has evolved. For instance, zebu cattle (*Bos indicus*) and taurine cattle (*Bos taurus*) have separate evolutionary lines. Zebu cattle have acquired physiological thermo tolerance due to body characteristics, metabolic modifications and genetic changes (60).

There is a marked conceptual difference between evolutionary adaptation and acclimatization; the first explains the genetic adaptation that involves changes in the animal and it requires the passage of hundreds and thousands of years. The second explains how changes are made to physiological mechanisms in order to maintain homeostasis (61).

Zebu cattle have a higher number of sweat glands, higher surface area of skin due to an increased number of skin folds that allow a more efficient transfer of thermal energy to the environment. Zebu cattle also have short white or grey hair that favors the reflection of sun rays rather than the absorption of heat as occurs in breeds with black or red hair. In addition, tissues have less resistance to the transfer of heat from body core to peripheral tissues, which favors convection and conduction processes for more efficient dissipation of body heat (62). Some researchers have shown that zebu cattle have a more extensive arteriovenous anastomoses than taurine cattle (63).

Metabolic adaptations in zebu cattle include lower energy requirements for maintenance compared with taurine cattle. Additionally, zebu cattle have lower generation of endogenous metabolic heat due to fewer intakes of forages, which decreases rumen fermentation and heat production. In effect, lower milk production (lactogenesis is

an exergonic process) and low secretion of thyroxine decrease general metabolism and body temperature (64).

Results of recent studies suggest that some cells, such as spermatozoa and oocytes, and embryos of zebu cattle are adversely affected to a lesser extent than taurine cattle in response to high ambient temperatures and those same cells are more resistant to the induction of apoptosis in zebu cattle. There is evidence that zebu cattle have acquired genes that protect cells from deleterious effects of high temperatures, although those genes have not been identified (60,65).

Alternatives to Reduce Heat Stress in Tropical Environments

Livestock in Colombia occupies about 75% of the agricultural land in areas where it has replaced native forests and has negatively impacted biodiversity and forests, compacted and eroded the soil, which, in some areas, has led to desertification over time (66). This is mainly due to low production efficiency in extensive systems based on monoculture grasses (66). An alternative to achieve this goal is the implementation of sustainable production systems, within which the use of silvopastoral systems (SPS) has been described as a successful strategy (66). SPS is an association of pasture, with fodder shrubs and trees, providing shade and higher levels of animal welfare (67); it also has been found that SPS reduces the impact of heat stress in cattle on both meat production (68) and milk (69).

In 2012, Tarazona (70) found that SPS offers better means to reduce environmental stress in bovines in three different ecosystems. The main reasons were the presence of good-quality water in a constant way, all the animals had access to it, a lot of places with shade and a major interchange of heat with circulating vegetation.

Conclusion

In conclusion, exposure to heat stress affects neuroendocrine response by inducing the secretion of adrenaline, noradrenaline, corticosteroids, growth hormone, renin and thyroxine. This hormonal alteration has metabolic consequences such as increased availability of energy for the animal to cope with the adverse situation. Prolonged exposure to stressful situations affect different response mechanisms, reducing growth by altering reproductive activity, threatening vital functions and compromising animal welfare.

Heat stress is a condition whose physiological impact could generate health problems in animals and particularly in mammals compromising production efficiency, so it is important to ensure optimum environmental conditions (presence of shadows, infrastructure, water and food) to favor allostatic animal responses to this type of aggression.

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Conflicts of interest

The authors declare that they have no conflicts of interest with regard to the work presented in this report.

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