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Review article

Heat Stress in Water Buffaloes: A Review. II Hypothalamic Neuromodulation of Thermoregulation

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ABSTRACT

Background: Water buffalo farming in tropical areas faces a paradox: its rustic adaptability contrasts with the physiological challenges of maintaining efficient thermoregulation in the presence of high air temperatures (AT) and relative humidity (RH). The impact of this binomial on livestock is best interpreted through the Temperature-Humidity Index (THI). The effect is amplified by the interaction with other climatic factors that increase the thermal sensation of heat, affecting animal welfare and reducing both productive and reproductive performance of this genetic pool. Moreover, the anatomophysiological characteristics of the skin reduce the thermoregulatory system's responsiveness to heat stress (HS). However, this can be improved through management systems that promote animal welfare by facilitating body heat dissipation in response to rising THI. This adverse condition increases the energy priority toward hypothalamic neuromodulation to maintain homeothermy. The physiological response to heat stress (HS) triggers a generalized alarm reaction from the hypothalamus, activating control systems that regulate the animal's body temperature. **Aim.** To analyze the hypothalamic neuromodulation mechanism governing thermoregulation through the lens of General Adaptation Syndrome, conceptualized as a comprehensive physiological response to heat stress in the water buffalo.

Development: The particularities of neuromodulation within the thermoregulatory system are analyzed from the comprehensive perspective provided by the General Adaptation Syndrome, in relation to the physiological response to heat stress in the water buffalo.

Keywords: water buffalo, heat stress, thermoregulation, neuromodulation, General Adaptation Syndrome (*Source*: *AIMS)*

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INTRODUCTION

The breeding of water buffalo has increased globally in recent decades as an alternative for producing high-value biological food intended for human consumption (Bertoni *et al*., 2019). In developing countries, water buffalo farming serves as an option to diversify livestock production due to its adaptive plasticity to various ecosystems (Bertoni *et al*., 2021), its role in ecosystem recovery (Bittel, 2022), and its efficient digestion of low-quality grasses, which are unsuitable for other livestock species (Javed *et al*., 2022).

The hardiness of the water buffalo allows it to adapt with a certain degree of proficiency to the conditions of the humid tropics (De León *et al*., 2022), including greater resistance to infectious and parasitic diseases (Grazziotto *et al*., 2020).

However, these animals are susceptible to heat stress (HS) in tropical environments (Gonçalves *et al*., 2021; Petrocchi *et al*., 2023) due to the morphological characteristics of the skin layer (Mitat *et al*., 2024), which limit their ability to dissipate heat through this route. The physiological strategy under these conditions increases rectal temperature (RT), heart rate (HR), and respiratory rate (RR) (Younas *et al*., 2020), while also inducing metabolic and behavioral changes (Athaíde *et al*., 2020).

In the water buffalo, the respiratory rate (RR) increases from 26 to 87 as the air temperature (AT) rises from 27°C to 35°C (Pereira *et al*., 2020). If AT exceeds 40°C, the increase in respiratory rate (RR) is insufficient to dissipate the necessary heat. Moreover, the increase in RR presents a disadvantage due to the greater heat production by the inspiratory/expiratory muscles and the risk of respiratory alkalosis under these conditions (Cartwright *et al.*, 2023).

Therefore, intensive water buffalo farming should incorporate facilities designed to promote thermal comfort, maintaining AT between 13.0°C and 24.0°C and a relative humidity (RH) between 55% and 60% (Vilela *et al*., 2022).

The growing interest in the development of water buffalo in tropical regions demands consideration of physiological alternatives that balance metabolic energy demand with the thermolytic capacity of this genetic pool. In this context, the General Adaptation Syndrome and its impact on the neuroendocrine response of the organism provide a systemic approach to evaluating the hypothalamic response to heat stress in the water buffalo.

This review aims to analyze the hypothalamic neuromodulation mechanism that regulates thermoregulation as an integral physiological response of the General Adaptation Syndrome to heat stress in the water buffalo.

DEVELOPMENT

Global warming poses an endemic challenge for livestock (Napolitano *et al*., 2023a) due to climatic factors that trigger heat stress (HS) in tropical regions. The effect of the interaction between high AT and RH (Thornton *et al*., 2022) defines the countries of Latin America and the Caribbean, where 1.23% of the global water buffalo population is reported (Bertoni *et al*., 2021). Under different climatic conditions, the negative impact on animal welfare can affect 10% to 30% of its productive performance (Kiktev *et al*., 2021).

In this context, some studies have evaluated the thermal comfort zone based on the Temperature-Humidity Index (THI) and the capacity of hypothalamic neuromodulation to regulate body temperature in the water buffalo.

The impact of the environment on the physiological capacity to dissipate heat and maintain homeothermy in the water buffalo in tropical regions: thermal comfort zone and THI.

The tropical climate is characterized by high and persistent AT, equal to or exceeding 18°C, with an average between 23°C and 24°C, and a thermal amplitude of 10°C, which can surpass 31°C due to perpendicular or near-perpendicular solar radiation and abundant precipitation throughout most of the year, affecting livestock welfare and milk production (Geiger *et al*., 1995). Cuba's geographical location, near the Tropic of Cancer, results in high solar radiation throughout the year, intensifying thermal sensation in the environment. This is accompanied by a humid seasonality and a higher maximum AT, ranging from 20°C to 31°C during the rainy season from May to October (Weather institute of Cuba, 2025). In Cuba, the climate in 2023 was characterized by an average temperature of 29.25°C, resulting from global warming, along with an increase in precipitation and RH (Fonseca *et al*., 2024). These conditions pose a challenge for HS in water buffalo due to the morphological characteristics of their skin, which include thickness, black coloration, high melanin content, low distribution of hair follicles, and sweat glands—factors that compromise heat dissipation (Mitat *et al*., 2024).

The water buffalo has a heat tolerance limit up to AT of 46°C, although the RH value under these conditions has not been specified, despite being a critical factor in assessing HS. Indeed, there is evidence supporting the thermoregulatory plasticity of the water buffalo and its high adaptability to tropical conditions, provided it has access to flooded areas for immersion and shade (Mota-Rojas *et al*., 2021a). Other sources of variation in heat tolerance are related to racial differences, physiological strategies for mitigating HS, and environmental conditions (Habimana *et al*., 2023). When environmental conditions exceed these thresholds, and the rectal temperature (RT) of the water buffalo surpasses the physiological range of 37.5°C to 39°C (Pereira *et al.*, 2020), a chain reflex physiological reaction is triggered from the hypothalamus, involving the cardiovascular, respiratory, endocrine systems, the skin, and metabolism, alongside behavioral changes (Picón *et al*., 2020). The modification in the priority of available energy aims to restore homeothermy, prevent the consequences of HS, and avoid its impact on animal welfare (Trapanese *et al.*, 2024).

The water buffalo is generally recognized as a species well-adapted to tropical conditions, within its thermal comfort zone, which corresponds to AT between 13°C and 24°C and RH ranging from 55% to 60% (Vilela *et al*., 2022).

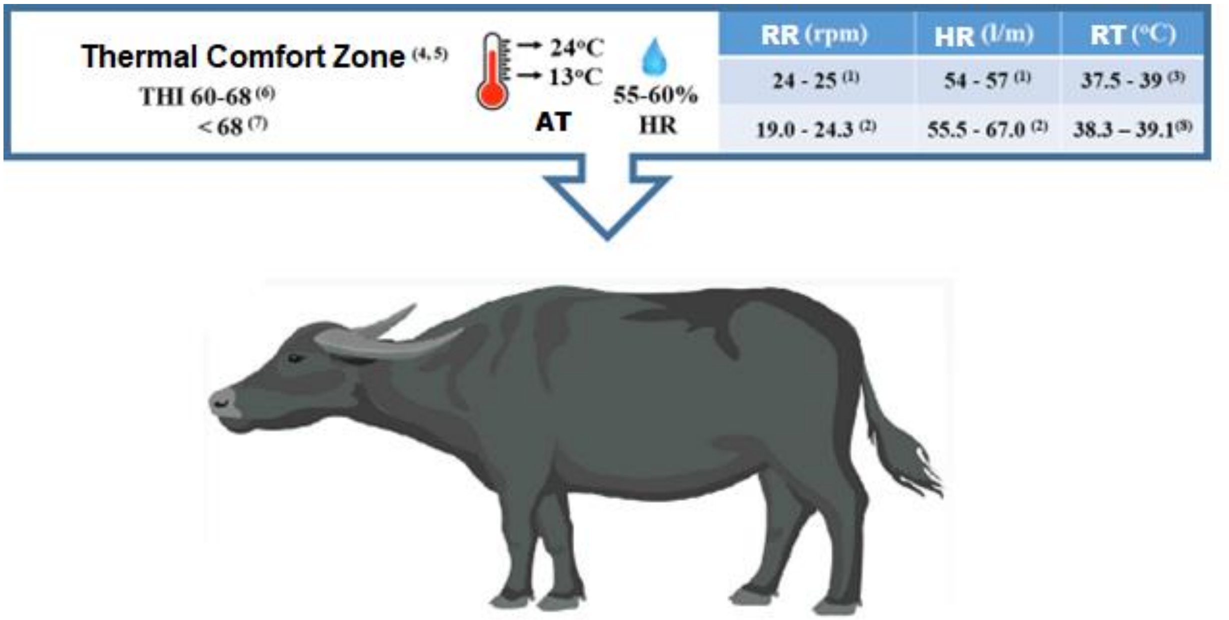

Figure 1. Physiological indicators in the thermal comfort zone of the water buffalo.

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(1) Parámetros fisiológicos y valores hematológicos normales en búfalos (Bubalus bubalis) del Magdalena Medio colombiano. Londoño, C.; Erika Natalia Sánchez, E.N. y Germán Alonso, G.A. (2012). Rev. Med. Vet. ISSN 0122-9354 N.º 23 January-June pp. 51-64. http://www.scielo.org.co/pdf/rmv/n23/n23a06.pdf.; **(2)** Pérez, M.E. Y Toro, E.N. (2008). Determinación de los parámetros hematológicos de búfalos machos adultos entre tres y diez años (bubalus bubalis): Nariño University Faculty of Agricultural Sciences. Pasto-Colombia. https://sired.udenar.edu.co/12279/1/75119.pdf.; **(3)** Mota-Rojas, D., Napolitano, F., Domínguez, A. *et al*., (2024). Calentamiento global y la conducta de los búfalos de agua. Ed. Abril-mayo. https://bmeditores.mx/ganaderia/revistas/entorno-ganadero-abr-24; **(4)** Vilela, R.A., Lourenço, Jacintho, M.A.C., Barbosa, A.V.C., Pantoja, M.H., Oliveira, C.M.C. and García, A.R., (2022). Dynamics of Thermolysis and Skin Microstructure in Water Buffaloes Reared in Humid Tropical Climate—A Microscopic and Thermographic Study. Front. Vet. Sci. 9, 871206. https://doi.org/10.3389/fvets.2022.871206.; **(5)** Napolitano, F.; De Rosa, G.; Chay-Canul, A.; *et al*., (2023). The Challenge of Global Warming in Water Buffalo Farming: Physiological and Behavioral Aspects and Strategies to Face Heat Stress. Animals, 13, 3103. https://doi.org/10.3390/ani13193103.; **(6)** José, N., Mota-Rojas, D., Napolitano, F. *et al*., (2021). Pérdidas de Calor Corporal y Efecto del Estrés Térmico en Búfalos de Agua. Suplemento Búfalo de agua 2021, 18 (112): 72-80. https://www.researchgate.net/publication/359683231_Perdidas_de_Calor_Corporal_y_Efecto_delEstres_Termico_en_Bufalos_de_Agua_Suplemento_Bufalo_de_agua_2021_18_112_72-80.; **(7)** Umar, S.I.U., Konwar, D., Khan, A. *et al*., (2021). Delineation of temperature-humidity index (*ITH*) as indicator of heat stress in riverine buffaloes (Bubalus bubalis) of a sub-tropical Indian region. Cell Stress and Chaperones 26,657–669. https://doi.org/10.1007/s12192-01209-1.; **(8)** De la Cruz, L., Maitre, E., Gasperín, J., Guerrero, I. y Mota-Rojas, D. (2014). El bienestar del búfalo de agua en sistemas agrosilvopastoriles. Entorno Ganadero Nº 65. BM Editores. https://www.produccion-animal.com.ar/informacion_tecnica/razas_de_bufalos/108-Sistemas_Agrosilvopastoriles.pdf

ITH is a frequently used indicator to assess the physiological impact of HS in livestock. An increase in ITH above 67 to 70 in water buffalo leads to a significant rise ($p < 0.05$) in RT, RR, and HR, including heat dissipation through both insensible and sensible pathways, (Sharma *et al.*, 2023) surpassing the thermal comfort zone for this species. The attempt to increase heat loss triggers the reflex arc of hypothalamic neuromodulation to regulate body temperature.

Hypothalamic neuromodulation of the thermoregulatory system

Living beings are an open system that exchange and transform matter and energy with their environment. The subsystem that regulates body temperature in endothermic animals develops thermolysis through two modalities, depending on the climatic conditions of their environment. As long as body temperature exceeds that of the environment, animals dissipate heat through radiation, convection, and conduction. However, when the air temperature exceeds body temperature, evaporative thermolysis becomes the primary mechanism for maintaining homeothermy.

Despite the fact that the gradient between core temperature, skin, and the environment is the physical phenomenon that determines the activation of hypothalamic neuromodulation to maintain homeothermy in the organism, it is not frequently specified in reviews addressing this topic.

Neurophysiological bases

Reflex neuromodulation in the water buffalo triggers a species-specific physiological response when heat-sensitive thermoreceptors detect an increase in AT (Mota-Rojas *et al*., 2021b). Mammalian skin has rich sympathetic innervation with a wide distribution of peripheral thermal receptors, represented by Ruffini corpuscles, located in the dermis, and central thermoreceptors found in large blood vessels, viscera, the spinal cord, and the preoptic area of the hypothalamus (POA) for core temperature regulation (Picón *et al.*, 2020). The family of transient receptor potential (TRP) cation channels is located in the dermis for the perception of AT and cellular signaling (Zhang *et al*., 2023). TRPV1 and TRPV2 receptors are sensitive to drastic heat elevation, while TRPV3 and TRPV4 detect temperature changes within a harmless range for mammals (Lezama *et al*., 2022). Among them, vanilloid receptors (TRPV, TRPV1, TRPV2, TRPV3, TRPV4) predominantly exist in the dermis, initiating the thermoregulatory response through peripheral vasodilation in the water buffalo (Napolitano *et al.*, 2023).

The increase in AT causes the depolarization of heat-sensitive receptors in the skin, generating the action potential of the afferent impulse, which reaches the laminae of the dorsal horn of the spinal cord. The nerve impulse travels through the spinothalamic tract, the trigeminal pathway, and the anterolateral columns of the spinal cord. For central thermoreceptors, the afferent pathways include the Goll and Burdach fasciculi, the spinothalamic tract, autonomic fibers, and the anterolateral columns of the spinal cord (Picón *et al*., 2020). The nerve impulse travels to the parabrachial nucleus and the midbrain, reaching the hypothalamus, where it projects onto heat-sensitive neurons in the preoptic area (POA) of the hypothalamic thermoregulatory center (Bienboire *et al*., 2023). The POA of the hypothalamus contains 30 to 40% of thermosensitive neurons, which become excited upon receiving signals from peripheral and central thermoreceptors when air temperature increases (Lezama *et al.*, 2022). In this way, the thermoregulatory center integrates the afferent peripheral and central nervous signals into the organism's overall response to maintain homeothermy, which includes the interaction between the hypothalamus, the limbic system, and the cortex (Sanmiguel & Díaz, 2011). From here, the high degree of integration for hypothalamic neuromodulation of thermoregulation is activated by the impact of HS on the body. This response contains two alternatives: The reflex pathway at superficial and deep levels (Gómez *et al*., 2022) contributes to the energy balance/metabolic activity of homeothermy, while the conscious pathway regulates thermoregulation through cortical perception, translating into a volitional thermolytic action with behavioral changes when leaving the thermal comfort zone.

The vegetative efferent pathways emerge from POA of the hypothalamus to reach the effector organs. In general terms, the effector organ of the reflex arc for thermolysis is the skin, which integrates the dual function of receptor/effector, where peripheral vasodilation is reinforced by sweating (Mota-Rojas *et al*., 2021[b]) to promote insensitive and sensitive heat loss. Peripheral vasodilation simultaneously stimulates tachycardia and thermal polypnea, reinforcing thermolysis (Chikkagoudara *et al*., 2022). Experimental evidence indicates that the water buffalo primarily resorts to vasodilation (García *et al*., 2023), which it employs with greater intensity and frequency for thermolysis through evaporation over more prolonged periods when compared to Bos taurus cattle (Pereira *et al*., 2020). The authors reported, in the same comparison, a higher frequency of HS signs in water buffalo, including panting (+29%), tongue protrusion (+27%), and neck extension (+27%).

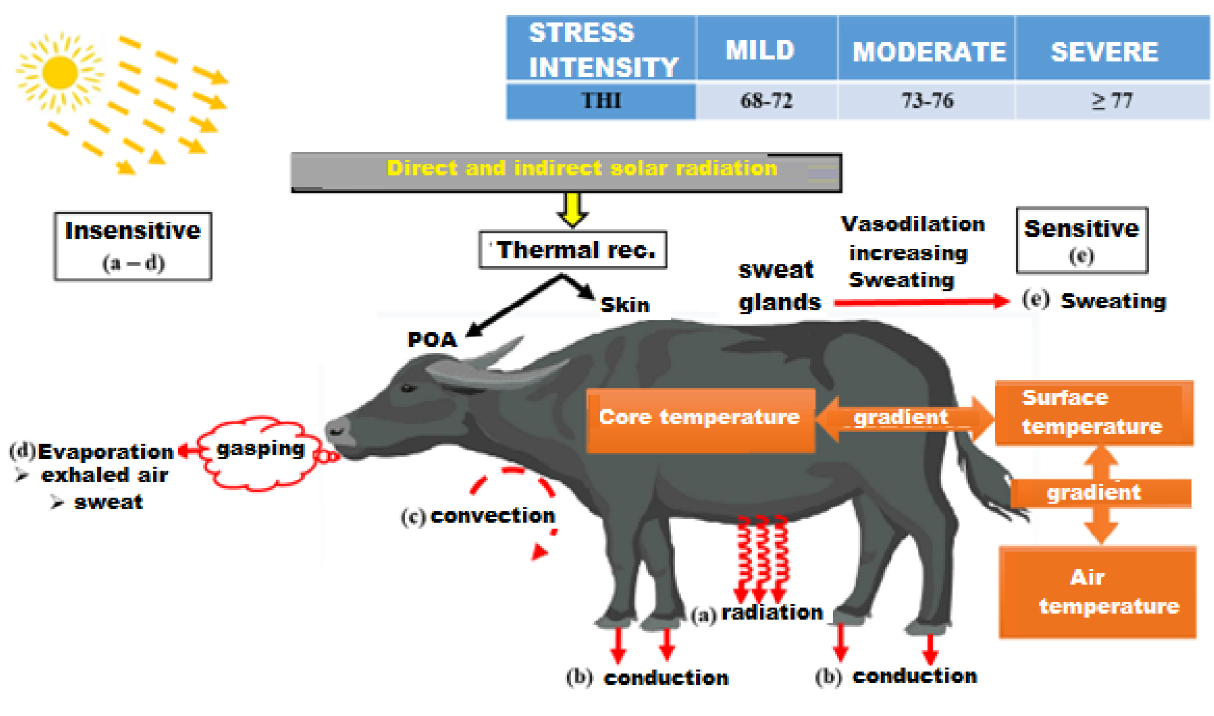

Figure 2. Activation of insensitive (a-d) and sensitive (e) thermolytic pathways in HS due to an ITH increase in the water buffalo.

Furthermore, the water buffalo has the disadvantage of low sweating capacity due to the scarce distribution of sweat glands in its skin (Mitat *et al*., 2024). However, available information on the sweating rate in this species is limited, which adds value to assessing its transpiration capacity in the search for genetic pools with greater heat tolerance under tropical conditions.

General Adaptation Syndrome (GAS)

The studies addressing hypothalamic neuromodulation of thermoregulation in water buffalo do not comprehensively focus on the General Adaptation Syndrome (GAS) in this context (Selye, 1973), the global endocrine response, the neurophysiological basis of the parallel increase in activity of the bulbar respiratory and cardiovascular center linked to POA of the hypothalamus, and the integrated perspective of the dual function of the skin as both a receptor and effector organ.

- **GAS phases**

Alarm-like reaction

During GAS, in the Alarm Reaction phase, the animal responds with an immediate adaptation mechanism through an increase in catecholamines, triggered by the activation and release of norepinephrine from the locus coeruleus and the hypothalamic-sympathetic-medullary-adrenal (HSMA) axis. The consecutive effect is characterized by an increase in RR and HR, vasoconstriction, mydriasis, distress, and suffering. These actions linked to the limbic system and the cortex determine a behavioral change aimed at preserving animal health and well-being (Damián *et al.*, 2020) through conscious neuromodulation, which reinforces the reflex pathway.

Resistance phase

The “Resistance” phase enables a longer-lasting adaptation process, involving glucocorticoids and other hormones. In this phase, the thermoregulatory strategy of the water buffalo is defined due to HS. In parallel, cortisol produces adverse effects, characterized by a reduction in immunocompetence and an increase in the incidence of diseases that affect the well-being and productivity of livestock (Chucuri *et al*., 2023).

Additionally, the impact of HS on the water buffalo affects hormonal stress biomarkers, completing the hypothalamic neuromodulation circuit of thermoregulation with an increase in catecholamines, cortisol, and vasopressin, alongside a reduction in thyroid secretion profile.

In buffalo, the activation of the locus coeruleus and the hypothalamic-pituitary-adrenal (HPA) axis in response to HS with an ITH greater than 82 increases peripheral cortisol concentration and oxidative stress (Li *et al*., 2020), which promotes the catabolism of carbohydrates, proteins, and lipids to provide energy and compensate for the reduced intake in that situation (Irreño *et al.*, 2022). In line with this, Lopez *et al*. (2021) reported higher levels ($p<0.05$) of capillary cortisol—51.52 ± 5.52 pg/mg—in Holstein dairy cattle, reflecting the chronic effect of HS during the August/September period, when the ITH reached its highest value.

Additionally, vasopressin from the paraventricular nucleus of the hypothalamus promotes heat dissipation through both evaporative and non-evaporative pathways in response to changes in the osmotic pressure of body fluids and renal filtration (Romero *et al.*, 2011).

Thyroid hormones (TH), thyroxine (T_4) and triiodothyronine (T_3), play a crucial role in regulating body temperature due to their calorigenic effect. They increase the metabolic rate by enhancing mitochondrial oxygen consumption, remodeling metabolism, and supplying energy to tissues. The neurons of the paraventricular nucleus (PVN) of the hypothalamus decode internal and external signals related to energy metabolism and thermogenesis/thermolysis, which mediate the release of thyrotropin-releasing hormone (TRH). In this way, it regulates the hypothalamic-pituitary-thyroid (HPT) axis for TH release. Consequently, the increase in AT (34≥40°C) suppresses the release of TRH, which in turn inhibits the hypothalamic-pituitary-thyroid (HPT) axis in an attempt to readjust the metabolic rate and maintain homeothermy (Kahl *et al.,* 2015). The consecutive reduction in plasma T_3 concentration, which has greater biological activity compared to T_4, is associated with the cattle's ability to tolerate HS (Pereira *et al*., 2008). In a comparative study between Nili-Ravi buffaloes and Holstein *Bos taurus* heifers, which evaluated the effects of artificial shade, showers, and forced convection, researchers found not only a significant difference ($p<0.05$) in favor of buffaloes—showing lower skin temperature, respiratory rate, and heart rate—but also higher TH concentrations (Younas *et al*., 2020). Previously, it was found that the ITH, RR, and HR were higher, while peripheral TH levels were lower ($p<0.05$) during the rainy season, which represents the peak HS for Holstein heifers in Cuban tropical conditions. In the same study, when grouping heifers with better thermoregulatory capacity (55.5% of the total, based on RR, HR, and RT), a correlation was found with medium (22.2%) and high (33.3%) circulating levels of T_3 (Pérez, 2000). This means that this hormone enabled the differentiation of two response strategies in heifers that exhibited greater heat tolerance. From this point, thermoregulation in relation to oxygen consumption at the cellular level is linked to thyroid metabolism, AT, and RT in a parallel pathway. However, compensatory mechanisms exist to modulate heat dissipation through peripheral vasodilation, RR, HR, and sweating rate.

The recovery phase provides a comprehensive framework for better understanding and assessing the increase in heat loss and the reduction in heat production, as well as their consequences in buffaloes. This evaluation takes into account the advantages and disadvantages that characterize this genetic pool and its adaptation to tropical conditions. Chronic HS induces immunosuppression, affects productive and reproductive efficiency, and increases livestock vulnerability (Sanmiguel & Díaz, 2011).

Unfortunately, most of the available information linking the impact of HS to TH in water buffalo is limited to describing its effect on the gland (Pérez *et al*., 2021) or differences in total serum T_4 and T_3 concentrations according to experimental conditions (Younas *et al*., 2020). A circadian, seasonal, individual, and genetic background-based study of the thyroid profile would allow for a deeper understanding of the impact of HT on water buffalo under tropical conditions.

Most studies addressing HS in water buffalo in tropical regions focus on evaluating RT, RR, and HR as immediate expressions of environmental conditions Thus, monitoring behavior as a physiological expression of an internal need in response to HS would further contribute to the understanding of conscious neuromodulation, promoting well-being and productive/reproductive efficiency in this species.

Exhaustion Phase

Finally, the "Exhaustion" phase is a critical stage in which the ability to adapt to the stressor is lost, negatively impacting health due to the functional failure of vital organs, leading to a generalized systemic breakdown (Selye, 1973). HS in livestock is triggered by increased solar radiation when the temperature exceeds the thermal comfort zone, and endogenous heat production surpasses dissipation through reflex neuromodulation and behavioral responses (Napolitano *et al.*, 2023).

In dairy cattle, selection and genetic improvement in high-producing females with a higher metabolic rate increase intolerance to HS. Currently, this represents a complex challenge for the dairy industry (Correa *et al*., 2022).

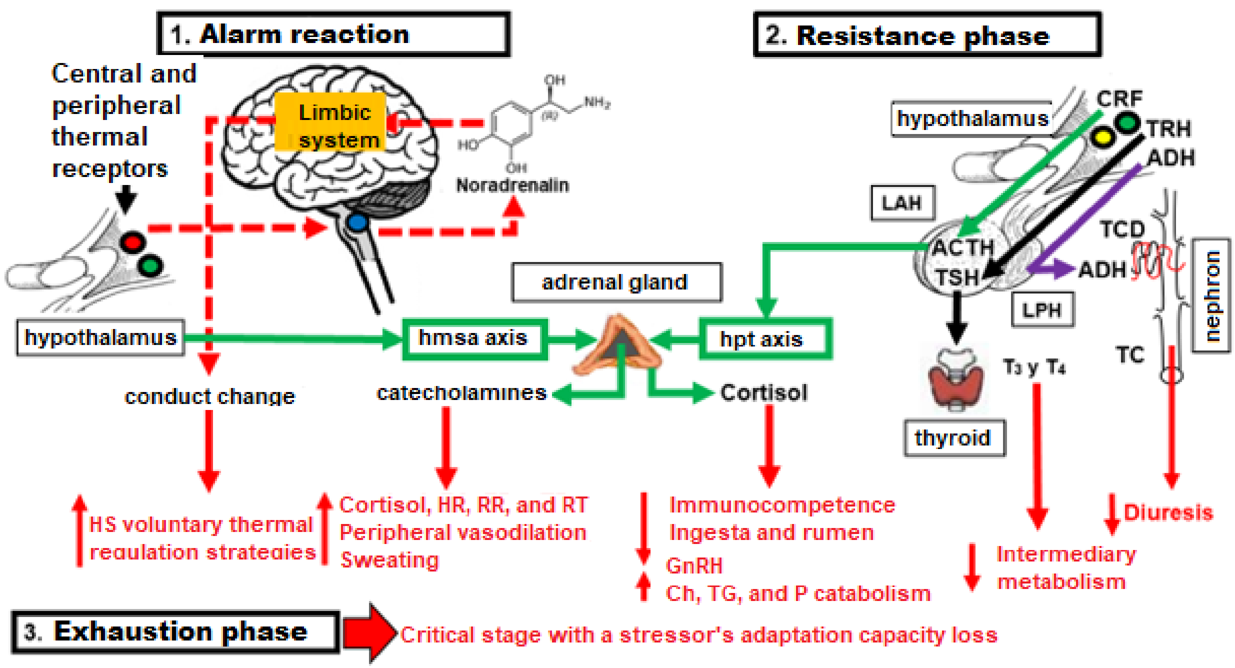

Figure 3. General Adaptation Syndrome due to heat stress in water buffalo

LEGEND

POA **Thermoregulator core** · **Paraventricular core** · **Coeruleus core** · **Supraoptic core**

TRH **Thyrotropin releasing factor**
TSH **Thyrotropic hormone**
CRF **Corticotropin release factor**
ACTH Corticotropin
ADH **Antidiuretic hormone**
HSMA **hypothalamus sympathic adrenal spinal cord axis**
HR, RR, RT heart rate, respiratory rate, rectal temperature
T3 y T4 **Triiodothyronine and thyroxine**
GnRH **Gonadotropin releasing factor**
HHMA **Hypothalamus hypophysis cortico adrenal axis**
TCD y TC **Distal contoured tube and nephrone collecting tube**
CH, TG y P **Carbohydrates, triglycerides, and proteins**
LAH y LPH **Anterior and posterior lobe of hypophysis**

There is consistency in the understanding that the water buffalo is a heat-tolerant species well adapted to tropical environments. However, when THI exceeds the threshold, hypothalamic neuromodulation mechanisms are activated for heat dissipation through all pathways, with the added complexity of the advantages and disadvantages for thermolysis in this genetic background (Mota-Rojas *et al.*, 2023). At this stage, raising buffalo in production systems with access to shade and water immersion is crucial for mitigating HS and ensuring thermal well-being. Moreover, enriched production systems bring animal welfare closer to the species' innate behavior, promoting alignment between sustainable farming conditions and the productive purpose. This approach could improve reproductive indices as well as buffalo meat and milk production in tropical regions (El Sabry & Almasri, 2022).

Under these conditions, HS is associated with reduced food intake, metabolic changes, and increased susceptibility to diseases (Trapanese *et al*., 2024). In lactating females, the incidence of mastitis may increase, affecting both the quantity and quality of milk (Napolitano *et al.*, 2020). The available information suggests that further research is needed to emphasize the importance of modifying the environment to mitigate the effects of high temperatures and direct solar radiation on the well-being, as well as the productive and reproductive efficiency, of water buffalo in tropical regions.

Another alternative is the development of genetic pools with improved heat tolerance under tropical conditions. This perspective is relevant, bearing in mind that the selection of high-producing breeds in tropical regions must align the maximum productive capacity of the appropriate genetic background with environmental and management conditions.

The entire physiological strategy described for the endocrine system as a regulator of bodily functions strengthens the adaptive response to HS in livestock. Considering that central role of the endocrine system in hypothalamic neuromodulation of homeothermy, then it would be more comprehensive to refer to neuroendocrine modulation rather than neuromodulation, as it is commonly designated.

CONCLUSIONS

The neuromodulation of thermoregulation in water buffalo is a highly complex physiological mechanism due to the interaction between the hypothalamus, the nervous and endocrine systems, and the species' own ability to regulate body temperature under tropical conditions. Hypothalamic neuromodulation of thermoregulation, viewed through the lens of the 'General Adaptation Syndrome,' presents a more comprehensive approach to neuroendocrine interaction. This mechanism helps mitigate the chronic effects of heat stress, which otherwise impair the metabolic and productive performance of the buffalo. Despite the plasticity of this genetic pool in maintaining homeothermic balance under tropical conditions, the implementation of good practices to mitigate excessive heat stress is essential to ensure animal welfare, which translates into improved productive and reproductive efficiency.

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AUTHOR CONTRIBUTION STATEMENT

Research conception and design: HPE, AMV, ALV; data analysis and interpretation: HPE, AMV, ALV; redaction of the manuscript: HPE, AMV, ALV.

CONFLICT OF INTEREST STATEMENT

The authors state there are no conflicts of interest whatsoever.