

Heat stress tolerance in Indonesian cattle: Genetic basis, physiological mechanisms, and reproductive performance (Review Article)

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ABSTRACT

Heat stress is one of the main environmental factors affecting the productivity and reproductive performance of cattle in tropical regions. Local cattle in Indonesia and other tropical countries have varying levels of adaptation to high temperature and humidity conditions, which are reflected in physiological responses and molecular mechanisms. Physiological indicators such as respiratory rate, rectal temperature, and heart rate, combined with reproductive parameters such as calving interval, days open, and conception rate, are often used to evaluate the impact of heat stress. At the molecular level, a number of candidate genes have been identified as playing a role in the heat stress response, including HSP70, ATP1A1, BCKDHA, HSPB6 and MYO1A, which are associated with cellular protection, antioxidant, and stress hormone regulation mechanisms. This article reviews the physiological and genetic basis of heat stress tolerance in tropical local cattle, as well as its implications for maternal reproductive performance. The review was undertaken to integrate existing knowledge and provide a comprehensive understanding of the interaction between genetic and physiological factors under conditions of heat stress. The expected outcome is the identification of potential biomarkers that can be applied in cattle breeding and management. This understanding is expected to support genetic marker-based local cattle breeding programmes, in order to improve heat stress resistance while maintaining reproductive productivity in tropical regions. The findings ultimately serve as a scientific foundation for the formulation of policies and the development of sustainable livestock strategies in tropical countries.

Introduction

The rise in global temperatures due to climate change has become a serious challenge for the livestock sector, particularly in tropical regions that experience high temperatures and humidity throughout the year. Heat stress negatively affects animal health, productivity, and, most importantly, reproductive performance in cattle, which is key to the sustainability of breeding operations. Local cattle in tropical regions, including Indonesia, the Thailand, and other Asian countries (Kajaysri and Wattananorasate 2018; Reeve et al., 2024; Liang et al., 2025), generally have better adaptability than imported breeds. However, this adaptability is often accompanied by a significant decline in production and reproductive performance under extreme heat stress.

The impact of heat stress on female cattle includes hormonal dysfunction, changes in the estrous cycle, reduced fertility, increased calving intervals, and higher rates of early embryonic death. This demonstrates a strong relationship between the physiological responses of cattle to environmental temperature and their reproductive performance. The Temperature Humidity Index (THI) has been widely used to assess the degree of heat stress in livestock (Fathoni et al., 2022). During the summer, heat stress affects the reproductive processes of dairy cattle at every stage, from the beginning of breeding to the later phases of pregnancy (Togoe and Mincă, 2024).

In addition to physiological aspects, molecular mechanisms also play an important role in adaptation to heat stress. Candidate genes such as Heat Shock Protein (HSP70 and HSP90) are known to help maintain protein stability and protect cells from heat damage, while other genes such as ATP1A1 and SOD are related to ion homeostasis and antioxidant defenses (Elayadeth-Meethal et al., 2021; Hu et al., 2022). The selection of these genes as molecular markers is predicated on their essential functions in cellular protection, oxidative stress regulation, and hormone

receptor activity (Rakib et al., 2024). Consequently, they are regarded as promising biomarkers for assessing heat stress tolerance and reproductive resilience in tropical cattle. Identifying these genes provides significant opportunities to develop molecular markers for breeding programs aimed at producing local cattle that are more heat-tolerant. To maintain homeostasis in unfavorable conditions, ruminant groups undergo physiological, endocrine, and behavioral changes to mitigate stress (Kim et al., 2022; Tanuwiria et al., 2022).

This review was conducted due to the significant challenges posed by heat stress in tropical livestock production. In the context of heat stress tolerance in cattle in Indonesia, a comprehensive review encompassing genetics, physiological mechanisms, and reproductive performance is crucial. This is because Indonesia, as a tropical country, faces significant challenges related to the impact of heat stress on cattle productivity and welfare. Furthermore, the integration of physiological responses with genetic markers in local Indonesian cattle remains underexplored.

By synthesizing available evidence, this article is expected to provide a better understanding of cattle adaptation to tropical climate conditions and also serve as a foundation for the development of more effective management strategies and breeding programs to improve heat tolerance in cattle in Indonesia. Thus, this review has the potential to make a substantial contribution to the sustainability and efficiency of the cattle farming industry, particularly in Indonesia. Furthermore, this paper aims to address this knowledge gap and offer clearer guidance for future research and breeding strategies (Rashamol et al., 2018; Sammad et al., 2020).

This review article sought to examine the physiological and genetic underpinnings of heat stress tolerance in tropical local cattle, alongside its implications for female reproductive performance. The anticipated outcome is to establish a scientific framework applicable to genetic improvement programs, reproductive management, and the development

of climate-resilient livestock policies in Indonesia. Through a comprehensive understanding, it is intended that genetic-based breeding strategies and enhancements in environmental management can be devised to augment the productivity and sustainability of cattle farming in tropical regions.

Effects of Heat Stress on Physiological Mechanisms and Reproduction

Heat stress is a condition of imbalance between the proportion of heat obtained from various sources, such as body metabolism, environmental influences, and the heat dissipation system, which can trigger an increase in body temperature in cattle (Brandl-Brown, 2018). Heat stress in cattle directly impacts the thermoregulatory system (Collier et al., 2019), changes in physiological systems (Koolhaas and Reenen, 2016), metabolism and nutrition, cellular responses, and implications for production and reproductive performance (Lucy, 2019). In tropical countries like Indonesia, heat stress is predominantly caused by environmental conditions such as high temperature and humidity. Heat stress from the environment is perceived by thermal receptors in the skin and internal organs. These stimuli are then transmitted to the hypothalamus, specifically the preoptic and anterior lobes, which function as the body's temperature-regulating center (Fig. 1). The hypothalamus detects that body temperature exceeds the physiological threshold, triggering activation of the autonomic nervous system to increase peripheral vasodilation and respiration rate in an effort to dissipate heat. In addition, the hypothalamus also regulates the release of neuro-hormonal factors in the form of releasing hormones which will influence the activity of the pituitary gland.

terior pituitary to produce adrenocorticotrophic hormone (ACTH), causing the adrenal glands to increase cortisol production (Collier et al., 2017). Cortisol helps provide energy by mobilizing the body's energy reserves, but its effects also suppress the immune system and reproductive function. Second, the hypothalamic-pituitary-thyroid (HPT) axis, through the release of thyrotropin-releasing hormone (TRH), stimulates the secretion of thyroid-stimulating hormone (TSH). Under conditions of heat stress, the production of TSH and thyroid hormones (T_3 and T_4) decreases, suppressing basal metabolism to reduce body heat production. Third, the hypothalamic-pituitary-growth (GH) axis, which normally stimulates the release of growth hormone (GH), decreases its secretion in heat-stressed cattle, disrupting growth rates and protein deposition.

These neurohormonal changes significantly impact the physiological condition of beef cattle. Increased heart rate and respiration occur as compensatory mechanisms, while hormonal changes, including increased cortisol and decreased GH, T_3 , T_4 , and insulin, disrupt energy metabolism, reduce feed consumption, and weaken the immune system. Consequently, production performance declines, characterized by decreased feed intake, daily body weight gain (ADG), and feed efficiency. Furthermore, reproductive function is also affected, for example, by decreased sperm quality in males and disruption of the estrous cycle in females (Khan et al., 2017). Thus, the body temperature regulation mechanism, initiated in the hypothalamus and continued through pituitary hormone secretion, plays a central role in determining the physiological response of cattle to heat stress, which ultimately significantly impacts their health, growth, and productivity.

Metabolically, cattle experiencing heat stress tend to reduce feed consumption, reducing energy availability. The body adapts by suppressing lipogenesis and increasing the breakdown of reserve fat (lipolysis), which in the long term can reduce body fat reserves. Furthermore, the efficiency of protein utilization is also impaired, resulting in increased muscle protein deposition and decreased body weight gain. In general, there is a decrease in fat deposition, an increase in protein catabolism, and a shift in metabolism toward emergency energy use.

To dissipate heat, cattle's bodies primarily utilize evaporation. Because cattle have relatively few sweat glands, they primarily lose heat through panting respiration, where water evaporation from the respiratory tract helps reduce body heat. This process is often accompanied by increased fluid and electrolyte loss, leading to the risk of dehydration. These physiological changes have direct implications for production performance. Feed intake decreases, daily body weight gain (ADG) decreases, feed efficiency deteriorates, and carcass quality is reduced. Furthermore, reproduction is also impaired due to the combination of hormonal stress, energy deficits, and metabolic disturbances. Therefore, the body temperature regulation mechanism, starting from the hypothalamus and extending to metabolic and evaporative responses, determines the cow's

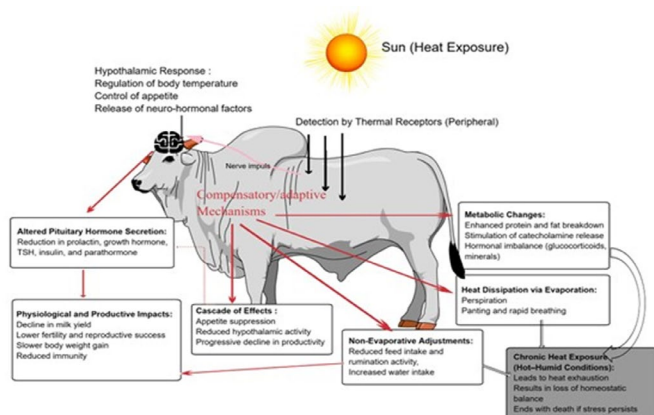


Fig. 1. Physiological mechanism during heat stress in cattle.

Pituitary activation then occurs through several main axes. First, the hypothalamic-pituitary-adrenal (HPA) axis, where the hypothalamus releases corticotropin-releasing hormone (CRH), which stimulates the an-

Table 1. Physiological response of Indonesian local cattle in heat stress area.

Cattle type	Research Locations	Microclimate Conditions	Rectal temperature (°C)	Respiration rate (breath/min)	Pulse rate (beats/min)	Reference
Bali	South Sulawesi, Indonesia	Ta: 32.90 °C; RH: 67.50 %; THI: 85.19	38.51	36.38	95.5	Sukandi et al. (2023)
PO	South Lampung, Indonesia	Ta: 34.29°C; RH: 64.50%; THI: 86.65	38.58	33.5	70.65	Adhitia et al. (2022)
Madura	East Java, Indonesia	Ta: 34.12°C; RH: 56.78%; THI: 84.56	38.58	33.75	88.5	Irmawanti et al. (2022)
Simental Cross	DKI Jakarta, Indonesia	Ta: 36.34°C; RH: 52.50%; THI: 86.98	38.53	55.67	71.33	Azzahra (2024)
Limousin Cross	Central Lampung, Indonesia	Ta: 34.72°C; RH: 48.60%; THI: 84.02	38.41	32.73	82.5	Erdisa (2024)
Brahman Cross	South Lampung, Indonesia	Ta: 34.29°C; RH: 64.50%; THI: 86.65	38.92	34.47	76.19	Adhitia et al. (2022)

Ta = Temperature ambient (°C).

ability to cope with heat stress, which ultimately significantly impacts its health, growth, and productivity.

Physiological Response of Local Cattle to Heat Stress

Physiological parameters, including respiratory rate, rectal temperature, and heart rate, serve as critical indicators for assessing cattle responses to heat stress. Table 1 provides a summary of the physiological responses of Indonesian local cattle in regions experiencing heat stress. The physiological responses of Indonesian local cattle and crossbred cattle under heat stress conditions reveal notable differences in adaptive capacity (Table 1). Local breeds such as Bali, filial Ongole (PO), and Madura generally maintain relatively stable rectal temperatures around 38.5°C despite being exposed to a high Temperature Humidity Index (THI > 84). Bali cattle, for instance, exhibited a rectal temperature of 38.51°C with a respiration rate of 36.38 breaths/min and a pulse rate of 95.50 beats/min at a THI of 85.19 (Sukandi et al., 2023). Similarly, PO cattle under THI 86.65 showed a comparable rectal temperature (38.58°C) but with a lower pulse rate (70.65 beats/min), indicating a more efficient respiratory mechanism for maintaining homeostasis (Adhithia et al., 2022). Madura cattle also demonstrated a similar rectal temperature (38.58°C) at THI 84.56, but with a higher pulse rate (88.50 beats/min), suggesting a greater reliance on cardiovascular adjustments to cope with heat load (Irmawanti et al., 2022). Madura and Bali cattle have an adaptive advantage due to their relatively small body size and larger body surface area, resulting in more efficient heat dissipation. According to Agustina and Hidayat (2025). Madura cattle maintain body temperature and respiration within a tolerable range under hot conditions. This observation is further supported by the heat tolerance coefficient, as the values recorded for Bali cattle 2.27–2.58 (Suhendro et al., 2022) are lower than those of Madura cattle 2.62 ± 0.2 (Yosit et al., 2016), despite both breeds being raised under the same tropical climatic conditions. Conversely, Simmental and Limousin cross cattle are more sensitive to heat, with rectal temperatures >39.5°C and respiratory rates reaching 65–80 breaths per minute, indicating strained thermoregulatory mechanisms. Their large, muscular bodies reduce heat dissipation capacity. Meanwhile, skin morphology between *Bos indicus* and *Bos taurus* show differences in sweat gland density and

structure, skin thickness, and other features that account for the superior thermoregulation of *Bos indicus*. These traits provide the biological basis for the strong heat tolerance of breeds such as Brahman (Jian et al., 2013). In line with Nursita et al. (2020), Ongole crossbred cattle (*Bos indicus*) exhibit the greatest sweating rate, whereas Simmental cattle (*Bos taurus*) show the lowest.

In contrast, crossbred cattle of European origin displayed more variable physiological responses. Simmental crossbred cattle in Jakarta, at a THI of 86.98, recorded the highest respiration rate (55.67 breaths/min) while maintaining a rectal temperature of 38.53 °C, indicating a greater sensitivity to heat stress and reliance on increased evaporative cooling through respiration (Azzahra, 2024). Limousin crossbred cattle in Central Lampung, however, presented the lowest rectal temperature (38.41°C) with a relatively moderate respiration rate (32.73 breaths/min), although their pulse rate remained high (82.50 beats/min), suggesting a distinct adaptive strategy (Erdisa, 2024). Interestingly, Brahman crossbred cattle, despite being recognized as a tropical breed—showed the highest rectal temperature (38.92°C) among all types at a THI of 86.65, accompanied by moderate respiration and pulse rates (Adhithia et al., 2022).

Indonesian local cattle exhibit superior adaptive capacity under heat stress compared with European crossbreds. Local breeds tend to maintain thermal stability more efficiently through balanced respiratory and circulatory adjustments, whereas crossbreds rely more heavily on increased respiration to dissipate heat. These physiological differences provide valuable insights for breeding strategies, reproductive management, and sustainable cattle production systems in tropical environments.

The Impact of Heat Stress on Reproductive Performance in Broodstock

Local cattle breeds, including Bali, PO, and Madura, generally exhibit superior reproductive efficiency compared to crossbred cattle in hot and humid environments. Specifically, Bali cattle in Jambi demonstrate a calving interval of 13.07 months, days open of 112.40, and 1.90 services per conception (Sari et al., 2021). Similarly, PO cattle in East Java present a slightly longer calving interval of 13.36 months and days open of 130.88 days, yet with a lower service per conception of 1.72, indicating relatively good fertility despite environmental challenges (Ardiyansyah et al.,

Table 2. Reproductive performance of Indonesian local cattle in heat stress area.

Breed	Research Location	Calving interval (months)	Days open (days)	Service per Conception (times)	Reference
Bali	Jambi	13.07	112.4	1.9	Sari et al. (2021)
PO	East Java	13.36	130.88	1.72	Ardiyansyah et al. (2023)
Madura	East Java	12.93	108.97	1.49	Rizki et al. (2025)
Simmental Cross	East Java	13.5	142.63	1.74	Ardiyansyah et al. (2023)
Limousin Cross	East Java	13.89	146.48	1.74	Ardiyansyah et al. (2023)
Brahman Cross	East Java	15.42	176.6	3.3	Sari (2025)

Table 3. Candidate Genes and Physiological-Reproductive Responses of Cattle Breeds under Heat Stress Conditions.

Gene	Breed	Mechanism related to heat stress	Relevance to physiology and reproduction	Reference
HSP70	Bali Cattle	HSP70.1 expression & polymorphism's associated with physiological responses to heat	Thermotolerance markers in local Indonesian (Bali) cattle; ability to maintain cellular function	Suhendro et al. (2024)
ATP1A1	Jabres, Bali, Galekan and Madura Cattle	Polymorphism associated with increased heat tolerance through Na^+/K^+ -ATPase activity	Increase in rectal temperature, respiratory rate	Prihandini et al. (2022)
BCKDHA	Madura, PO and Bali Cattle	Missense mutations; changes in the amino acid sequence and signal peptide	Adaptation to dry climate	Farajallah et al. (2024)
HSPB6	Sahiwal Cattle	Potential use as a selection marker for heat tolerance	Increased respiratory rate and rectal temperature	Kumar et al. (2022)
MYO1A	Chinese Cattle	Missense mutation; significant association with heat tolerance trait	Increase in Temperature Humidity Index (THI)	Jia et al. (2019)

2023). Among the local breeds, Madura cattle exhibit the most efficient reproductive performance, characterized by the shortest calving interval of 12.93 months, the lowest days open of 108.97 days, and the lowest service per conception of 1.49, reflecting a strong adaptive reproductive capacity in hot climates (Rizki et al., 2025). In contrast, crossbred cattle exhibited suboptimal reproductive performance under similar heat stress conditions. Specifically, Simmental crossbred cattle had a calving interval of 13.50 months, days open of 142.63 days, and required 1.74 services per conception (Ardiyansyah et al., 2023).

Limousin crossbred cattle experienced an even longer calving interval of 13.89 months and days open of 146.48 days, with a comparable service per conception rate of 1.74, indicating delayed conception and extended postpartum anestrus. The most pronounced reproductive inefficiency was observed in Brahman crossbred cattle, which exhibited a significantly prolonged calving interval of 15.42 months, days open of 176.6 days, and the highest service per conception rate of 3.3, suggesting considerable reproductive challenges despite the Brahman's general reputation as a heat-tolerant tropical breed (Sari, 2025). Indonesian cattle breeds exhibit superior reproductive resilience under conditions of heat stress when compared to European crossbreds and certain tropically adapted breeds. The enhanced performance of Bali, PO, and particularly Madura cattle can be attributed to prolonged natural selection and adaptation to local climatic conditions, which promote efficient reproductive physiology and resilience to environmental stressors. Conversely, the extended calving intervals and increased services per conception observed in crossbred cattle indicate a heightened susceptibility to heat-induced reproductive impairments, such as diminished oocyte quality, impaired follicular development, and reduced conception rates.

The mechanism of stress on reproductive performance

High temperatures and humidity will cause heat stress in cows, resulting in redistribution of blood flow. Blood flow to internal organs such as the uterus decreases, while blood flow to the skin and extremities increases. As a result, there is an increase in uterine temperature and a decrease in hormone perfusion to uterine tissue. In addition, endocrine disturbances resulting from the processes that control gonadal development and function can delay ovarian follicular development, increasing foetal and embryonic loss. Heat stress factors bind to heat shock protein (HSP) gene promoters, which rapidly increase expression in heat-stressed cells, inducing protective mechanisms. More specifically, HSP70 production increases with pregnancy development, serving to stabilise protein structures and thereby inhibit translational factors that induce apoptosis. The potential for embryo loss increases when cows experience heat stress during pregnancy. High temperatures and humidity cause blood flow redistribution, affecting the physiological regulation of the oviduct and uterus. Blood flow to internal organs such as the uterus decreases, while blood flow to the skin and extremities increases. As a result, there is an increase in uterine temperature and a decrease in hormone perfusion to uterine tissue. This causes a decrease in specific protein synthesis as a result of disturbances in the physiological regulation of oviduct and uterine function. Embryo loss during pregnancy in cows is caused by a decrease in the synthesis of specific proteins by the embryo due to prolonged exposure to high temperatures (Sakatani, 2017).

Genetic and Physiological Interactions in Heat Stress Adaptation

Exposure to heat stress in cattle triggers a series of physiological changes in an effort to maintain body homeostasis. Increased environmental temperature, reflected in the temperature–humidity index (THI), causes an increase in rectal temperature, respiration rate, heart rate, and changes in feed consumption behavior (Yetmaneli et al., 2020). These

physiological responses are regulated by molecular mechanisms at the cellular level, primarily through the induction of heat shock proteins (HSPs), such as HSP70 and HSP90, which act as molecular chaperones, protecting proteins from denaturation due to heat stress (Suhendro et al., 2024).

Several genes have been identified as playing significant roles in regulating physiological responses to heat stress, whether through protein stability, body temperature regulation, or other molecular mechanisms (Hariyono and Prihandini 2022). Identification of genetic polymorphisms in these genes provides an opportunity to develop marker-assisted selection (MAS) to improve heat tolerance in cattle populations (Rastosari et al., 2025). Several candidate genes have been studied and are associated with heat stress responses, including HSP70, ATP1A1, BCKDHA, ATP1B2, HSPB6, and MYO1A (Table 3).

HSP70 is one candidate heat stress gene that has been studied in local Indonesian cattle (Bali cattle) (Suhendro et al., 2024). The results showed that HSP70 expression increased significantly under heat stress conditions, and genetic polymorphisms in the promoter and 5'UTR regions were also identified. The HSP70 gene has been reported to influence expression levels and individual resistance to heat stress. This genetic variation explains individual and breed differences in adaptation to tropical environments. This strengthens the hypothesis that heat tolerance is not simply a temporary physiological response but is also influenced by genetic factors that determine long-term adaptive capacity. Therefore, measurements of physiological parameters such as rectal temperature and respiration rate need to be combined with molecular analysis to obtain a comprehensive picture of heat tolerance levels in local cattle. Conceptual framework in the relationship between heat stress, physiological response, candidate genes and reproduction showed in Fig 2.

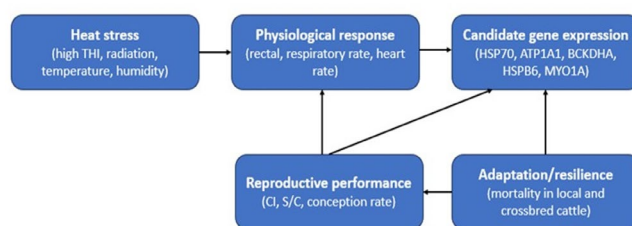


Fig. 2. Conceptual framework in the relationship between heat stress, physiological response, candidate genes and reproduction.

The impact of heat stress extends beyond physiological and molecular changes and also impacts reproductive function. Persistent increases in body temperature can disrupt oocyte development, reduce spermatozoa quality, and inhibit embryo implantation, all of which ultimately lead to decreased fertility (Pasha et al., 2024; Schüller et al., 2017). Molecular studies have shown that heat stress suppresses the expression of genes important in the reproductive pathway, including FSHR, LHCGR, and oocyte growth factors such as BMP15 and GDF9 (Collier et al., 2019). Therefore, the integration of physiology, genetics, and reproduction is crucial for comprehensively understanding the impacts of heat stress. Polymorphisms in the HSP70 gene, which affect protein stability and antioxidant mechanisms, for example, have the potential to be used as genetic markers for selecting cattle with improved heat tolerance without compromising reproductive performance. Therefore, an integrative approach between physiological data, gene expression, and reproductive performance is needed as a strategy for developing adaptive and productive local cattle in tropical regions.

Conclusion

Heat stress has a significant impact on the physiology and reproductive performance of cattle in Indonesia. The physiological mechanisms

involved include changes in body temperature, respiratory rate, heart rate, and sweat production. Local cattle generally show better tolerance to heat stress than imported cattle. Reproductive performance is reduced by heat stress, as evidenced by disruption of the estrous cycle, decreased fertility, and increased embryonic mortality. Several candidate genes, such as HSP70, ATP1A1, BCKDHA, HSPB6, and MYO1A, can be used as markers for heat stress traits. Adaptation strategies include environmental modification, feed management, and breeding programs to improve heat tolerance. Further research is needed to develop effective and sustainable heat stress mitigation methods and to identify genetic markers associated with heat tolerance in local Indonesian cattle. A better understanding of the mechanisms of heat stress tolerance can help improve livestock productivity and welfare in tropical regions.

Conflict of interest

The authors declare that there is no conflict of interest regarding the publication of this paper.

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