Thermoregulation in Sheep under Heat Stress: Postprint

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Abstract

Heat stress is induced by high-temperature environments. Under hot climatic conditions, when the effective ambient temperature exceeds the upper critical temperature of the thermoneutral zone in sheep, heat stress occurs. However, the adverse effects induced by heat stress are pervasive, not only severely compromising the welfare of sheep, but also resulting in elevated body temperature, reduced growth performance, compromised immune function, and deteriorated meat quality. This review summarizes the factors that induce heat stress in sheep and the thermoregulatory mechanisms under heat stress conditions. During heat stress, the body accumulates a substantial heat load through absorption of environmental radiant heat and accumulation of metabolic heat production, which surpasses the heat dissipation capacity. Sheep exposed to high-temperature environments can eliminate excessive heat load by enhancing heat dissipation. As homeothermic animals, when ambient temperature and humidity fluctuate, sheep and goats can maintain the balance between heat production and heat loss by adjusting their heat production, feed intake, water consumption, respiratory rate, and behavior. In conclusion, sheep can employ complex and effective heat dissipation mechanisms to maintain thermal balance and adapt to high-temperature environments.

Full Text

Heat Stress and Thermoregulation in Sheep and Goats

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Abstract

Heat stress is induced by high-temperature environments. In hot climates, when the effective ambient temperature exceeds the upper limit of the thermoneutral zone, sheep and goats experience heat stress. The adverse effects triggered by heat stress are widespread, severely impacting not only animal welfare but also causing elevated body temperature, reduced growth performance, compromised immunity, and decreased meat quality. This review examines the factors that induce heat stress in sheep and goats and the thermoregulatory mechanisms employed under such conditions. During heat stress, animals accumulate a high heat load through environmental radiant heat and metabolic heat production, which exceeds their heat dissipation capacity. Sheep exposed to high ambient temperatures increase heat dissipation to eliminate excess heat load. As homeothermic animals, sheep and goats maintain thermal balance by adjusting heat production, feed intake, water intake, respiratory rate, and behavior in response to changes in air temperature and humidity. In summary, sheep and goats utilize complex and effective heat dissipation mechanisms to maintain body temperature balance and adapt to high-temperature environments.

Keywords: sheep; goats; heat stress; thermoregulatory responses

1 Factors Causing Heat Stress

Heat stress is generally considered a physiological response to high environmental temperatures. Within the thermoneutral zone, animals rely on physical and behavioral regulation without activating biochemical mechanisms for thermoregulation, maintaining normal body temperature with minimal basal metabolic rate and energy expenditure. When temperatures exceed the upper limit of the thermoneutral zone, animals begin to experience heat stress, with increasingly severe responses at higher temperatures.

Energy exchange between animals and their environment is significantly influenced by environmental factors (ambient temperature, relative humidity, solar radiation, wind speed, precipitation), animal factors (breed, coat color, lactation stage, health status), and thermoregulatory mechanisms (circulatory regulation, sweating, panting, behavior).

1.1 Environmental Factors

In hot climates, high ambient temperature and humidity, intense direct and indirect solar radiation, and low wind speed are the primary environmental stressors causing heat stress in animals [1-4].

During heat stress, ambient temperature typically exceeds body surface temperature, causing animals to accumulate a high heat load through environmental radiant heat and metabolic heat production that surpasses their heat dissipation capacity [5]. When environmental heat load exceeds a specific critical temperature threshold, sheep cannot cool themselves or maintain physiological functions, resulting in heat stress. This manifests as increased rectal temperature and respiratory rate, leading to reduced body weight, average daily gain, growth rate, and total body solids content that reflect impaired regenerative capacity [6-10].

Solar radiation is a major factor affecting thermoregulation in grazing ruminants. Intense solar radiation during hot seasons rapidly reduces sensible heat loss in sheep. Without shade and the insulating effect of fleece, sheep absorb exogenous heat exceeding their metabolic heat production, disrupting thermal balance and causing severe heat stress [11]. Ewes exposed to solar radiation exhibit increased rectal temperature and respiratory rate, decreased plasma alanine aminotransferase and alkaline phosphatase activities, reduced potassium and magnesium concentrations, and elevated non-esterified fatty acid content and aspartate aminotransferase activity [12]. Yamamoto et al. [13] demonstrated in dairy cattle that radiation provides more heat load than actual air temperature.

Environmental humidity also contributes to heat stress, positively correlating with its severity. At high temperatures, animals primarily rely on evaporative heat loss, which is proportional to the vapor pressure difference between the animal' s evaporative surfaces (skin and respiratory tract) and the air. The vapor pressure at evaporative surfaces depends on surface temperature and moisture; higher skin temperature and moisture (e.g., from sweating) increase vapor pressure and facilitate evaporative cooling. However, as ambient vapor pressure increases, the gradient between surface and air vapor pressure decreases, reducing evaporative heat loss. Consequently, heat dissipation becomes more difficult in hot, humid environments, exacerbating heat stress. At 35 °C, increasing relative humidity from 57% to 78% raises ram body temperature by 0.6 °C [11], demonstrating that high humidity suppresses cutaneous evaporative cooling. While low relative humidity at the same temperature facilitates evaporative cooling and reduces stress, improving growth and production performance [14], high humidity significantly intensifies heat stress severity [7-9].

Wind speed primarily affects convective and evaporative heat loss. Increased wind speed accelerates convective cooling because good air circulation is essential for promoting heat loss through convection and facilitates insensible perspiration [14]. A wind speed of 3.5 m/s reduces serum cortisol concentration in summer, increases sheep activity, and decreases rectal temperature and respiratory rate, alleviating heat stress [15]. At high temperatures, increased wind speed benefits convective cooling as long as air temperature remains below skin temperature, though high wind speed under extremely high air temperature may actually promote heat gain. Regardless, increased wind speed always facilitates surface moisture evaporation, showing a positive correlation with evaporative heat loss.

According to Lee et al. [16], the order of importance for climatic factors affecting physiological parameters is: ambient temperature > solar radiation > humidity

> wind speed. Costa et al. [17] reported that the thermoneutral zone is 20-28 °C for goats and 21-25 °C for sheep. Kumar et al. [18] defined the climatic boundaries for goats' thermoneutral zone as: air temperature 13-27 °C, relative humidity 60%-70%, wind speed 5-8 km/h, and moderate solar radiation. Toussaint [19] recommended that appropriate indoor temperatures for dairy goats should be maintained at 6-27 °C (optimal 10-18 °C), with relative humidity of 60%-80% and wind speed of 0.5 m/s.

1.2 Animal Factors

The efficiency of thermoregulation in sheep and goats largely depends on breed and individual genetic differences. Variations exist among breeds in reducing metabolic and endogenous heat production while enhancing heat dissipation capacity [1-2]. Goats exhibit better heat tolerance than sheep due to stronger water retention capacity, smaller metabolic body size, lower basal metabolism, faster respiratory rate, and higher skin temperature, all facilitating heat dissipation [20]. Local breeds have strong adaptive advantages to their specific environments, while introduced purebreds may be particularly susceptible to heat stress due to limited adaptability [21]. Thermoregulation in newborn lambs is influenced by the ambient temperature experienced by the dam during pregnancy [22]. Additionally, lambs born to ewes that maintain lower rectal temperatures have higher birth weights than those from ewes with higher rectal temperatures [23], indicating that selecting dams that can maintain normal rectal temperature under heat stress will produce lambs with normal birth weights in hot climates.

Morphological differences play important roles in heat tolerance and thermoregulation. Short-haired goats exposed to solar radiation show substantial increases in rectal temperature, skin temperature, respiratory rate, and pulse, with lower feed consumption compared to long-haired goats [24]. Therefore, long-haired goats have better tolerance to solar radiation heat than short-haired goats. According to Finch et al. [25], black goats have advantages over white goats in resisting solar radiation in hot deserts. Although black coats absorb more solar radiation, black goats can forage in sunlight for longer periods. Under intense solar radiation, black goats absorb twice as much heat as white goats (exceeding 800 W/m^2) [26], resulting in higher body surface temperatures. However, this should not be considered a disadvantage because solar radiation absorption occurs primarily near the surface of the black coat, and the high surface temperature increases sensible heat flow at the body surface-air interface, especially with strong wind speeds that dissipate more heat. In white coats, solar radiation absorption occurs deeper in the fleece, causing the body to gain more radiant heat [27]. Additionally, black goats can drink water equivalent to approximately 35% of their body weight and effectively utilize evaporation for cooling, though no difference exists between coat colors in shade.

2 Thermoregulation Mechanisms Under Heat Stress

Heat stress represents the physiological response of animals to thermal environments, involving a series of activities in the nervous, endocrine, and immune systems. Under heat stress conditions, animals respond actively through self-regulation within certain limits. Thermoregulatory responses to heat stress are divided into two types: autonomic regulation and behavioral regulation.

2.1 Autonomic Regulation

Autonomic regulation refers to physiological responses controlled by the hypothalamic thermoregulatory center that adjust heat dissipation to maintain constant body temperature in response to thermal stimuli from internal and external environments. These responses include increased skin blood flow, altered respiratory frequency and pattern, and sweating. The hypothalamus receives information from peripheral and central nervous systems and initiates appropriate hormonal changes to maintain homeostasis. When animals encounter emergencies such as hunger, trauma, heat, cold, hypoxia, mental stress, or fear, sympathetic nervous system excitation and enhanced adrenal function occur, manifesting as sympathetic-adrenal medullary system hyperactivity with massive secretion of epinephrine and norepinephrine, triggering stress responses [28-29].

To maintain thermal balance, heat production and dissipation exist in dynamic equilibrium. Within the comfort zone, heat production and loss are essentially balanced. Heat sources include internal metabolic heat production and heat absorption from the external environment. Internal metabolic heat comprises basal metabolic heat, muscular activity heat, production-related heat, and heat increment, varying with lactation stage, production level, genetics, feed intake, and feed quality and type. External heat gain primarily originates from environmental sources. Within the thermoneutral zone, sheep maintain relatively constant body temperature through evaporation, conduction, and convection. When temperature exceeds the upper limit of the thermoneutral zone, thermal balance is disrupted, resulting in heat stress. High ambient temperature induces attempts to dissipate latent heat using different methods to balance excessive heat load. During heat stress, sheep tend to reduce internal metabolic heat production, accelerate heat dissipation, and minimize heat gain from the environment.

Under continuous high temperature conditions, sheep regulate blood flow through skin vessels by adjusting vasodilation and vasoconstriction to maintain thermal balance. During heat stress, blood redistribution from visceral to body surface areas increases cutaneous blood flow, raising skin temperature and the gradient between skin and ambient air temperature to enhance sensible heat loss, particularly during the initial phase of heat stress [1,30]. This is evident through significantly increased heart rate and correspondingly increased skin blood flow. Additionally, heat load increases plasma and body fluid volume proportionally to thermoregulatory demands [30], buffering temperature rise and enabling tolerance to longer periods of dehydration. In desert regions, heat-stressed goats maintain normal feed intake and milk production even after 48 hours of dehydration, related to their ability to sustain adequate blood flow to the intestines and mammary gland [31]. Therefore, increased body water content under hot climates represents an adaptive response that improves heat stress tolerance. Furthermore, during skin vasodilation, increased total blood volume and water content facilitate water permeation from capillaries into tissues and sweat glands, with blood flow velocity to the skin affecting sweating rate [32] to promote evaporative cooling from skin and respiratory tract. Significant hemodynamic changes may be attributed to two factors: increased muscle activity controlling respiratory rate along with elevated respiratory frequency, and reduced peripheral vascular bed resistance with arteriovenous shunting. These mechanisms maximize heat dissipation from skin and respiratory tract through radiation and conduction. Consequently, during heat stress, the body autonomically regulates increased blood flow to body surfaces and organs to enhance heat loss and maintain temperature stability.

High temperatures alter endocrine function in sheep. Circulating concentrations of hormones such as thyroid hormones can change according to environmental conditions [33-34]. These hormones directly participate in metabolic rate regulation and obligatory thermogenesis, making them important in temperature regulation. Reduced thyroid secretion and decreased thyroid hormone concentrations stimulate cells to reduce oxygen consumption and heat production, leading to decreased metabolic rate and basal metabolic heat production [35-36]. Koluman et al. [34] observed reduced serum thyroid hormone concentrations in sheep exposed to high temperatures, which can lower basal metabolic rate and prevent increased endogenous heat production.

Respiratory rate and rectal temperature are the most common indicators for evaluating adaptability and heat tolerance in hot weather because they relate to the most common heat exchange mechanisms between animals and their environment. The average body temperature of goats (at 23 °C ambient temperature) is 37.6 °C (37-39 °C), with rectal temperature varying between 38.3-39.0 °C [14]. Outside the thermoneutral zone, animals must activate thermoregulatory mechanisms. When these mechanisms fail, rectal temperature increases, leading to hyperthermia. An increase of even 1 °C or less in rectal temperature is sufficient to reduce growth or production performance in most livestock [37-38]. Compared to thermoneutral conditions, heat-stressed goats show higher rectal temperatures, with heat stress causing goats (Comisana [39-40] and Nubian goats [41]) to reach rectal temperatures of 40 °C or higher. Additionally, exposure of goats to high temperature and humidity significantly increases skin temperature in the neck, ears, and thighs. When ambient temperature rises, sheep ears and legs dissipate a high proportion of heat because these regions account for approximately 23% of body surface area. Due to direct contact with the environment, these areas are sensitive to environmental influences and show strong positive correlation with ambient temperature. When internal heat dissipation becomes difficult during elevated ambient temperature, heat load accumulates and skin temperature rises. Higher skin temperature increases the gradient between body surface and environment, improving heat dissipation efficiency and alleviating heat stress.

During heat stress, ambient temperature typically exceeds skin surface temperature, creating high heat load as animals gain substantial heat through convection and radiation. Under these conditions, water evaporation becomes the most effective cooling method, absorbing 2.43 kJ of heat per milliliter of water evaporated [2]. Sheep can tolerate external temperatures up to 43 °C for several hours through important thermoregulatory mechanisms such as sweating and panting [42]. However, ruminants have relatively underdeveloped sweat glands, and fleece impedes skin evaporative cooling. Therefore, sweating is far less important than respiratory evaporation for temperature regulation in high-temperature environments. When temperature rises beyond a certain threshold, sheep begin rapid breathing with open-mouthed panting, sometimes excessive salivation, reaching respiratory frequencies of 300-400 breaths/min compared to only 10-30 breaths/min at rest in cool conditions (12-20 breaths/min for sheep, 10-30 breaths/min for goats) [43]. As ambient temperature increases from 20 °C to 40 °C, goat respiratory rate rises from 30 to over 200 breaths/min, indicating the important role of respiratory water evaporation in heat dissipation. At thermoneutral ambient temperature (12 °C), goats dissipate only about 20% of total heat through respiratory moisture, but this can reach approximately 60% of total heat loss at ambient temperatures above 35 °C [44]. In Merino sheep at 40 °C, total evaporation is 250 $g/(m^2 \cdot h)$, while maximum skin evaporation is only 63 $g/(m^2 \cdot h)$, making respiratory evaporation more than three times greater than cutaneous evaporation [42]. Therefore, respiratory rate represents the primary heat dissipation pathway under high-temperature conditions and serves as an indicator of heat stress severity. Appleman et al. [41] observed that Nubian goats' thermoregulatory systems became ineffective after 12 days at 40 °C but not at 35 °C, concluding that the upper limit of heat tolerance in goats lies between 35-40 °C. When high relative humidity compounds high ambient temperature, sheep respiratory frequency further increases, related to elevated apparent temperature [45]. Under high ambient temperature, lamb respiratory rates can reach 400 breaths/min. However, when temperature rises sufficiently to inhibit respiratory evaporation, respiratory rate significantly decreases, stabilizing at 155-200 breaths/min with deeper panting than normal shallow breathing.

Since fetal development depends primarily on fetal metabolic heat production and heat exchange with the dam [46], under normal conditions (21-24 °C), fetal temperature in late-gestation goats (39.5 °C) is 0.6 °C higher than maternal core temperature (38.9 °C) [47]. When these goats are exposed to heat stress (40 °C and 60% relative humidity) for 2 hours, both fetal and maternal temperatures increase, but fetal temperature rises more slowly. This smaller increment may result from reduced uterine blood flow and fetal metabolic heat production due to hypoxia, potentially causing fetal malnutrition and ultimately intrauterine growth retardation.

2.2 Behavioral Regulation

Behavioral regulation refers to the maintenance of relatively constant body temperature through specific behaviors. In addition to altered feed and water intake patterns, this includes lethargy, reduced activity, seeking shade, avoiding overheated environments or moving toward suitable temperature zones, changing posture, and reducing movement and muscular activity. Behavioral regulation serves as a supplement to autonomic regulation.

Exposure to high ambient temperatures stimulates peripheral thermal receptors to transmit inhibitory neural impulses to appetite centers in the hypothalamus, suppressing the lateral appetite center and reducing feed intake [44,48]. Appetite functions as a thermoregulatory mechanism because feed intake is associated with heat production, particularly in ruminants where heat increment represents a significant source of body heat [2,41]. Feed intake should decrease as temperature rises to reduce heat production and keep animals cool. Therefore, reduced feed intake is a method to decrease heat production in warm environments. Mendes et al. [49] observed decreased dry matter intake in sheep (from 66.3 g/kg to 59.9 g/kg) under two temperature conditions (22-25 °C and 32-35 °C). Salama et al. [50] demonstrated that reduced feed intake during heat stress is not due to decreased feeding frequency (heat-neutral and heat-stressed goats both averaged 41 meals per day), but rather to a 40% reduction in meal duration, explaining lower feed intake under heat stress conditions.

During heat stress, sheep tend to reduce roughage intake while increasing concentrate consumption. Bhattacharya et al. [51] conducted a trial with sheep fed different roughage-to-concentrate ratios at low (11-22 °C) and high (27-32 °C) temperatures. The results showed that at a 75:25 roughage-to-concentrate ratio, ad libitum intake was highest at low temperature and lowest at high temperature (879 g vs. 447 g). At a 25:75 ratio, intake decreased to 758 g at low temperature and 652 g at high temperature. Thus, high temperature adversely affects feed intake, with this negative effect becoming more pronounced when diets have high fiber content. Additionally, roughage consumption time decreases with increasing air temperature and humidity [41,51]. Goats consume hay for an average of 16-19 minutes per hour at 20-35 °C, but essentially stop eating at 40 °C, while grain consumption also decreases at 40 °C. We hypothesize that during heat stress, sheep reduce roughage intake to decrease volatile fatty acid production, thereby reducing energy absorption and heat production to maintain body temperature.

Rumination time (including standing and lying rumination) decreases with increasing air temperature and humidity. Sheep spend approximately 46% of grazing or feeding time ruminating, with daytime rumination accounting for about 11% of total grazing time in grazing sheep [52]. According to Yousef [53], rumination is primarily influenced by the degree of environmental temperature variation, with absolute air temperature being secondary. Increasing temperature from 20 °C to 40 °C reduces the average rechewing rate in goats from 90 to 73 times/min.

Under thermoneutral conditions, feed intake is the primary determinant of water intake or turnover. Heat stress significantly increases water and ion losses in ruminants [54], thereby increasing their requirements. Brain thermal sensors and thirst-regulating sensors are associated with vasopressin release at the hypothalamic level, and heat defense mechanisms are adjusted according to the animal' s water balance [55]. Dehydration and increased solute concentration in body fluids of mammals exposed to high temperatures reduce thermoregulatory evaporation and increase body temperature [56]. This adjustment in thermoregulation has been observed in panting and sweating animals as a regulatory response to conserve water in dehydrated animals. In species like goats that both pant and sweat, progressive dehydration leads to reduced sweating and increased respiratory rate [56].

Heat stress increases water consumption in goats, with the additional water intake primarily used to increase heat loss through evaporation from skin (sweating) and respiration (panting) [57]. Increased respiratory frequency is accompanied by greater water evaporation and consumption, resulting in significant increases in both water intake and evaporation observed in goats [55]. Mendes et al. [49] observed increased water intake in sheep (from 2.13 kg/kg dry matter intake to 4.04 kg/kg dry matter intake) under two air temperatures (22-25 °C and 32-35 °C). Water consumption at 40 °C was significantly lower than the peak obtained at 35 °C. Water intake amount, frequency, and duration all increased [41]. Increasing ambient temperature from 20 °C to 38.0-39.5 °C for 5.15 hours decreased plasma sodium concentration and osmolarity in goats, indicating blood dilution. These results suggest that heat stress causes primary polydipsia in goats. Unlike sweating, panting does not cause loss of mineral salts, allowing better plasma volume maintenance. Another advantage of panting involves cooling blood passing through the nasal region, keeping brain temperature lower than deep body temperature. Therefore, water deprivation or restriction exacerbates heat stress effects. During heat stress, sheep increase water intake to replenish fluid losses and enhance heat dissipation through panting and sweating to reduce body temperature.

Altering behavior and posture represents another important thermoregulatory strategy. In high-temperature environments, sheep modify their behavior (e.g., seeking shade) and posture (e.g., standing perpendicular to the sun rather than lying down) to reduce heat gain from the environment and maximize heat dissipation to lower heat load. The primary circadian habit of ruminants is daytime activity and nighttime rest. However, during hot weather in tropical and subtropical Mediterranean climates, grazing ruminants tend to lie down and reduce daytime activity, preferring to graze before sunrise, at dawn, and at night. Seeking shade, particularly during hot daytime periods, represents a prominent form of behavioral adaptation in hot regions [30]. At high temperatures, sheep seek shade to reduce radiant heat gain from the environment and stretch their bodies to increase surface area for heat dissipation [7]. Without shade, animals alter their posture to a position perpendicular to the sun to reduce the effective area for heat exchange [58]. For cattle in direct sunlight, increasing air temperature from 16 °C to 18 °C reduces idle lying time and increases idle standing time. Sheep tend to huddle and stand closely side-by-side to reduce effective surface area and avoid gaining more solar radiation heat [52]. Standing reduces the area exposed to direct solar radiation compared to lying down, so livestock grazing on hot, arid rangelands with little shelter remain standing for extended periods rather than lying down when directly exposed to solar radiation [11]. Additionally, when standing, heat transfer with the ground occurs only through the small contact area of the feet, increasing the distance between skin and ground and reducing heat gain from hot surfaces. Under severe heat stress, animals wet their bodies with water or nasal secretions to increase evaporative cooling. In summary, animals regulate heat exchange with their environment through behavioral responses in high-temperature environments.

In conclusion, as ambient temperature, relative humidity, and solar radiation gradually increase while wind speed decreases, sheep experience increased heat production and reduced heat dissipation, resulting in heat stress. This manifests as increased rectal temperature and respiratory rate, electrolyte and enzyme system imbalances, and decreased growth and production performance. During heat stress, sheep regulate heat production and dissipation through autonomic and behavioral mechanisms to maintain thermal balance. These regulatory mechanisms do not operate independently but work synergistically to maintain constant body temperature. Specifically, heat-stressed sheep increase respiratory frequency and water intake to enhance respiratory evaporative cooling while reducing feed intake to decrease heat production. Additionally, they seek shade and alter standing or lying postures to reduce radiant heat gain. Thus, sheep can tolerate high temperatures and adapt to extremely hot environments. Given the complexity of thermoregulatory mechanisms under heat stress and variations in sheep breeds and climate patterns across different production regions, many research findings remain inconsistent. Current domestic and international research on sheep thermoregulation under heat stress has focused primarily on physiological and behavioral aspects. With rapid developments in transcriptomics and proteomics, some molecular mechanisms underlying heat stress effects on sheep thermoregulation have been investigated, but deeper and more systematic studies at the molecular level are still needed.

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Note: Figure translations are in progress. See original paper for figures.