

Physical and behavioural adaptability of sheep to thermal stress

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Abstract

Climate change-induced heat stress (HS) affects livestock productivity by limiting resources like feed, fodder, and water. Sheep rearing has become a viable animal husbandry practice in resource-constrained regions like arid and semi-arid regions, due to their ability to adapt to extreme weather, feed and water scarcity, and long migrations. Additionally, sheep are less susceptible to tropical diseases, further making them suitable for these regions. Sheep exhibits morphological, behavioral and physiological adaptation to HS, which allows them to escape the vagaries of thermal stress. The breeding and selection of animals with long legs, existence on scanty food and water and the adaptability to long-route migration are achieved in sheep. Sheep breeds with dark skin and light coat colour along with the optimal fleece length exhibit greater tolerance to heat, compared with woolly and dark coat colour sheep. Sheep decrease their feed intake and increase water intake, along with modification for behaviour like seeking shade, staying near water sources and exhibiting nocturnal habits of feeding in response to HS. In addition, heat shock proteins and their molecular pathways are activated to maintain homeostasis at the cellular level. The diurnal variation in body temperature, respiratory rate and stress hormones are observed for acclimatizing to HS. However, these adaptation strategies affect health and welfare as well as decrease the productivity of animals. Therefore, implementing effective strategies to mitigate heat stress-induced physiological complications in sheep is essential to enhance the sustainability and economic viability of the sheep production system.

Keywords: Adaptation, Behaviour, Coat colour, Small ruminants, Thermal stress

Highlights

- Sheep exhibit physiological and behavioural responses to thermal stress. Breeds in arid and semi-arid regions have undergone phenotypic modifications for adapting to the harsh climate.
- Coat and fleece colour play an important role in reflecting solar radiation.
- Heat stress modifies feeding, water intake, standing, lying and reproductive behaviour in sheep.

INTRODUCTION

Small ruminants play a significant role in the global economy by supporting the livelihoods of numerous people who raise them in diverse climates (Naqvi *et al.*, 2017; Danso *et al.*, 2024). Major sheep-producing countries, which include China, India, Australia, New Zealand and various nations in Africa, are likely to face very serious climate-related impacts in the next few decades including increases in temperature, frequent floods and water scarcity (I-IPoC, 2007). Climate change is expected to affect air temperature, precipitation patterns, water availability, and atmospheric carbon dioxide levels, which will adversely affect feed and fodder production as well as influence livestock productivity and sustainability (Rojas-Downing *et al.*, 2017). Additionally, climate change also poses a threat to food security by altering the frequency of events such as desertification, droughts and land degradation, as well

as the intensification of extreme weather phenomena especially high episodes of thermal stress (I-IPoC, 2019). When the equilibrium between heat gain and heat loss is disturbed, and the animals cannot dissipate body heat, they experience heat stress (HS) (Collier *et al.*, 2017). In fact, climate change driven HS has been regarded as one of the greatest constraints on livestock production worldwide (Collier *et al.*, 2017; De *et al.*, 2017c; Mitchell *et al.*, 2018).

Sheep farming has been a sustainable option for people in arid and semi-arid areas for centuries (De *et al.*, 2019a; McManus *et al.*, 2022). Sheep play a significant role in rural economies, especially in arid, semi-arid and mountainous areas, because of their multiple utility such as wool, meat, milk, skins and manure. Although there are low vegetation resources in these areas, sheep rearing has provided a sustainable livelihood option which sustains the rural population.

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In India, landless, small, and marginal farmers prefer small ruminants due to minimal space and management needs. Small ruminants like sheep are particularly suitable for small landholders in villages because of the low initial investment, ease of rearing the small ruminants and high feed conversion ratio, yielding high economic returns. Also, they flourish well in harsh climates and long migrations and have higher resistance against tropical diseases (Naqvi *et al.*, 2013).

Arid and semi-arid lands cover approximately 53.4% of the total land area of India, primarily comprised of rangelands. Eleven of the forty-two distinct sheep breeds are adapted to these environments. These breeds have traits that allow them to cope with extreme summer climates. This might be due to natural selection, which evolved the sheep according to the climatic conditions (Naqvi *et al.*, 2015). Moreover, sheep adapt to such adverse climatic conditions through behavioural, morphological, physiological and largely genetic modification (FAOSTAT, 2018; Berihulay *et al.*, 2019).

Different stressors under changing climatic scenario

In animal production systems, HS is a significant concern in semi-arid and arid regions. It affects livestock physiology, leading to reduced reproduction and production, as well as increased mortality (Hoffmann, 2010). To cope with the detrimental effects of HS, sheep adjust their physiological responses according to seasonal changes (De *et al.*, 2013; De *et al.*, 2017b; De *et al.*, 2019b). In addition to HS, nutritional paucity is another significant stressor in semi-arid regions (De *et al.*, 2019c; De *et al.*, 2021). In extensive production systems, the well-being of livestock is entirely dependent on herbage, which is directly affected by climatic extremes and seasonal fluctuations. The extreme heat during summer months worsens the nutritional scarcity in animals under pastoral systems, leading to under-nutrition during late spring and summer. This is primarily due to the increased energy expenditure for thermoregulation and a simultaneous decrease in energy intake (Sejian *et al.*, 2014).

In arid and semi-arid tropical environments, low biomass productivity is a significant constraint during the summer months (Sahoo *et al.*, 2015b). The availability of feed in rangelands is substantially reduced and often, it is not available during the dry season. Due to the low biomass density per unit area, sheep are forced to increase their grazing time and disperse more widely, resulting in long-distance walking to find feed (Naqvi *et al.*, 1991). This leads to walking stress, in addition to HS and feed scarcity, which can alter homeostasis and metabolism processes (Sejian *et al.*, 2012).

Water scarcity is another major concern in semi-arid

regions during the summer months (De *et al.*, 2015; Kumar *et al.*, 2016). The lack of good-quality drinking water is a common challenge for grazing animals (Naqvi *et al.*, 2015; Sahoo *et al.*, 2015a). Some breeds are reported to survive for 7 days with scanty to no water in hot arid and semi-arid areas (Chedid *et al.*, 2014; Nejad and Sung, 2017). Nevertheless, water shortages can negatively impact animal physiology, resulting in weight loss, reduced reproductive performance and increased vulnerability to diseases (Barbour *et al.*, 2005). In the field condition, most of the time, the above stresses, i.e., HS, nutritional stress, water stress and walking stress, occur simultaneously or in combinations (Kumar *et al.*, 2019) causing multiple stress (Naqvi *et al.*, 2017), which adversely affects the animal productivity and welfare.

Adaptation to stress and resource allocation

To negate the above-described adverse climatic effect, sheep try to adapt themselves to the changing climatic scenario. Adaptation is a dynamic and continuous process in which living organisms undergo phenotypic changes over time in response to various environmental stimuli. According to the Intergovernmental Panel on Climate Change (IPCC), adaptation refers to the initiatives and measures taken to reduce the vulnerability of natural and human systems to the actual or expected effects of climate change (Hoffmann, 2010). The animals acclimatize to their microenvironment during both the acute and chronic HS exposure, by expression of HS-induced genes and thus altering their molecular pathways to maintain cellular homeostasis (Bharati *et al.*, 2017a; Dangi *et al.*, 2017). However, both short- and long-term adaptation to HS involves multiple mechanisms, which ensures survivability against erratic thermal insults (Bharati *et al.*, 2017b). The normal physiological and metabolic pathways associated with resource allocation during thermal stress is indispensable for animal health and productivity (Rauw, 2009; Huber, 2018). The 'barrel model' of resource allocation proposes that resources must be prioritized between maintenance, growth, production, and reproduction during an animal's lifetime, depending on environmental and climatic conditions (Weiner, 1992; Huber, 2018). Moreover, HS releases stress hormones and activates inflammatory pathways, subsequently, the animals are immunosuppressed, which predisposes them to various metabolic and infectious diseases (Bharati *et al.*, 2017c; Jose *et al.*, 2022). It has been reported that selection and breeding intended for high-productivity farm animals have resulted in decreased fitness, disease resistance and climate change vulnerability, which has adversely

affected animal physiology and productivity, directly as well as indirectly.

Genetic adaptation for thermal stress is a slow process that occurs over many generations through natural selection (Ames and Ray, 1983). Adaptation traits usually exhibit low heritability. Therefore, selection programs for HS adaptability are problematic and cost intensive. For many breeds of sheep, several genes are responsible for heat tolerance; however, in each breed, selection for heat tolerance doesn't seem logical (Berihulay *et al.*, 2019). Sheep have the ability to adapt to different geographical and environmental conditions, including extreme and harsh climates (Al-Haidary *et al.*, 2012). However, in response to thermal stress, sheep exhibit morphological, behavioural, physiological and metabolic reactions (De *et al.*, 2017c; De *et al.*, 2023). The different aspects of adaptation in sheep are depicted graphically in Fig. 1. Over many generations, sheep have developed morphological adaptations, which are physical changes that improve their fitness in a given environment. Key morphological adaptations of sheep include body size and shape, coat and skin colour, hair type, and fat storage (Berihulay *et al.*, 2019).

Morphological modifications

Sheep breeds in arid and semi-arid regions have

undergone phenotypic modifications to adapt to the harsh climate. The sheep of these regions have long legs, which enables them to migrate long distances in search of vegetation resources as feed scarcity occurs during the lean period. Marwari and other western Rajasthan sheep migrate to eastern Rajasthan and Gujarat during periods of feed scarcity. Similarly, Dumi/Patanwadi sheep of Saurashtra migrate to Ahmedabad, Anand and adjoining areas during scarcity periods. This migratory behaviour has led to the intermixing of breeds, followed by the selection of farmers for migratory capability. For instance, the Kheri genotype has resulted from the mixing of Malpura sheep with Marwari inheritance (Naqvi *et al.*, 2013). Their large ears are also an anatomical adaptation thought to aid in convective heat loss (Degen and Shkolnik, 1978).

Hair, wool and thermoregulation

The hair coat serves as the primary interface between the body and the environment, playing a crucial role in regulating heat loss and gain. Coat reflectance, hair length and hair density are the key characteristics of hair that are directly related to heat exchange (McManus *et al.*, 2009; Castanheira *et al.*, 2010; do Prado Paim *et al.*, 2013). The hair structure protects against direct solar radiation and promotes convection and heat loss

through evaporation (Leite *et al.*, 2018). Hair type significantly impacts heat tolerance. Sheep with hair coats tolerate heat better than woolly breeds, especially in hot and humid tropical climates (McManus *et al.*, 2009). The fleece of native breeds helps maintain body temperature within a range despite high ambient temperatures, creating a microenvironment that acts as a thermal barrier (Eyal, 1963). The fleece is essential for adapting to extreme environmental conditions. Fleece act as a protective barrier and reduces heat loss through sweating by impeding the evaporation of water from the body (Wojtas *et al.*, 2014).

Thermoregulation is generally lower in wool sheep (Titto *et al.*, 2016) and shearing can further aggravate this effect. The carpet wool-type sheep found in semi-arid regions, thermoregulation is greatly contributed by convective heat loss from the skin to the environment (Degen and Shkolnik, 1978). When sheep are shorn, the insulating effect and protective function

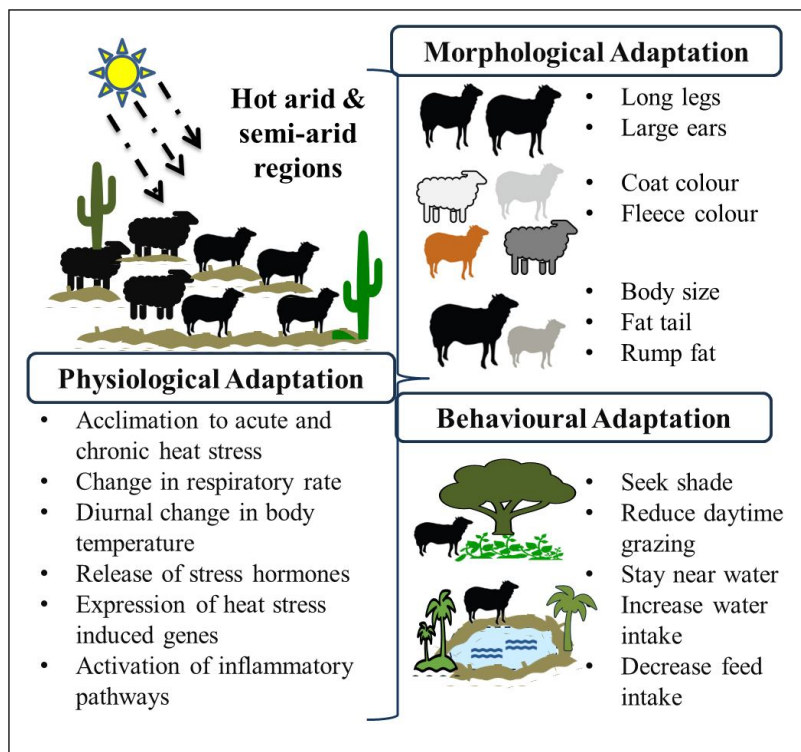


Fig. 1. Graphical representation of different aspects of adaptation in sheep in hot arid and semi-arid regions

of wool are diminished, leading to increased transmissivity and greater energy reaching the skin. Even with thinner wool, air stability within the fleece reduces heat loss by convection. However, some reports also propose that shearing reduces thermal stress in sheep (Pietro *et al.*, 2004; Dikmen *et al.*, 2011). Shearing improves heat transfer via conduction, convection and radiation (Berman *et al.*, 1985), as well as increased evaporative heat loss (McArthur *et al.*, 1980). These differences may be attributed to differences in breed and thermal adaptability to a particular climatic condition.

Skin, coat colours and thermoregulation

Coat and fleece colour also play a crucial role in reflecting solar radiation, keeping the skin cooler (Kay, 1997) and ultimately leading to thermoregulation without excessive water loss through panting (Degen and Shkolnik, 1978). The epidermis, the outermost layer of the skin, plays a crucial role in protecting an organism from the external environment (Feingold *et al.*, 2007). The radiant heat load as well as the amount of solar radiation absorbed by and reflected from the body is significantly affected by the coat colour (Daramola and Adeboye, 2009). Animals with light coat colours tend to absorb less heat than those with darker coats (Asres *et al.*, 2014). The coat and skin colour of sheep and goats that have evolved in tropical and desert areas differ from those in temperate climates (McManus *et al.*, 2020). The loose, open fleece of Awassi sheep helps to enhance heat loss through convection (Gootwine, 2011). Sheep with dark pigmentation are more prone to HS as compared to those with light pigmentation, implying that selecting animals with light coat colours can improve animal welfare and production efficiency (Fadare *et al.*, 2012). Breeds like Awassi and Omani sheep, have carpet-type wool, light-coloured fleece, thinner skin, shorter hairs, and fatter tails, which enable better heat dissipation in hot environments (McManus *et al.*, 2009).

Skin traits, including the percentage of epithelial area occupied by sweat glands, skin reflectance and thickness, are crucial for adaptation to HS (McManus *et al.*, 2009; 2022). It has been observed that animals having dark coats exhibit greater absorption of thermal radiation and, therefore, are more disposed to HS as compared to animals with light coat colours (McManus *et al.*, 2009; Fadare *et al.*, 2012). However, some studies have found conflicting results, suggesting that the relationship between coat colour and heat tolerance is complex and influenced by multiple factors (Titto *et al.*, 2016). Skin and coat traits act synergistically on heat tolerance traits in sheep, wherein the animals with darker skin and white coats exhibit higher tolerance to HS (McManus *et al.*, 2020).

Body size

Body size affects the thermal biology of ruminants and influences the energy requirement for maintenance, growth and production (Mitchell *et al.*, 2018; McManus *et al.*, 2022). Variations in body size also influence resilience to environmental change (Martin *et al.*, 2018). Body shape and size also influence the thermoregulatory mechanisms of animals in extremely hot environments (Silanikove, 2000). Animals adapt to environmental heat through variations in body size, such as large, small, or dwarf statures, which help regulate water loss and heat gain (Cain *et al.*, 2006). Larger animals have a lower metabolic rate than smaller animals and gain heat at a slower rate. In fact, body shape along with the appendages influences the rate of heat gain and loss. For instance, animals with long and narrow appendages reduce radiant heat gain but increase convective heat loss. Taller animals dissipate more heat than animals with short and squat bodies (Mwacharo *et al.*, 2006). Silanikove (2000) and McManus *et al.* (2020) stated that large animals have a lower metabolic rate, resulting in slower heat gain.

Additionally, animals with long, thin appendages reduce heat gain and increase heat loss, further aiding in thermoregulation (Mwacharo *et al.*, 2006). On the other hand, smaller animals, especially the hairy breeds, have a higher specific surface area, making them more vulnerable to solar radiation (West, 2003). However, some studies have found that smaller animals can be more heat-tolerant, with characteristics such as shorter, fewer and lighter hairs, as well as thinner skin (Seixas *et al.*, 2016). Taller animals, such as the Bighorn sheep, dissipate more heat than animals with short and squat bodies (Cain *et al.*, 2008). Morphological modifications, such as body shape and size, have also evolved to reduce heat load and minimize water loss. Small ruminants in semi-arid regions are smaller in size compared to European breeds, which allows for a larger surface area for better heat dissipation (Naqvi *et al.*, 2013). Singh *et al.* (2017) found that Indian sheep breeds with smaller sizes, white and lustrous coats, dark skin colour and hair coat were more adaptable to HS.

Fat storage

Tail fat and rump fat are often considered adaptive responses of animals to extreme environments (McManus *et al.*, 2022), serving as valuable energy reserves during migration and in times of feed unavailability during climatic extremes (Moradi *et al.*, 2012). Notably, approximately 25% of the world's sheep population consists of fat-tailed breeds (Moradi *et al.*, 2012). Well-adapted breeds exhibit specific localized fat deposition, particularly in the tail. This external

localization of fat allows better heat dissipation by other organs (Degen and Shkolnik, 1978). The fat tail constitutes a vital energy reserve for some sheep breeds in arid and semi-arid regions, especially during episodes of food and water scarcity, thus safeguarding survivability and productivity (Chilliard *et al.*, 2000; Atti *et al.*, 2004). Some fat-tailed breeds are extensively used as maternal breeds in tropical conditions, and they have the ability to accumulate and mobilize body fat in internal fat depots (Chay-Canul *et al.*, 2011).

Behavioural adaptation

Sheep exhibit various behavioural adaptations to cope with thermal stress (Nejad and Sung, 2017). They start panting (De *et al.*, 2017c) and breathe with an open mouth during severe heat stress. Most researchers highlighted that ruminants are active during the day and rest at night, protect themselves from extreme environmental factors by dissipating body heat through hairlessness, shedding, water restriction and feed intake (Attia, 2016; Koluman *et al.*, 2016). However, as per Dwyer (2009), they change diurnal behavioural patterns and become more active at night. This might be due to higher degree of stress. Sheep generally reduce daytime grazing in warm weather. To avoid heat gain, sheep change their behaviours, such as seeking shade (Sherwin and Johnson, 1987; De *et al.*, 2020d) and avoiding overcrowding (Silanikove, 2000).

Feeding and water intake

The feeding behaviour of animals is essentially affected by the environment. High temperatures reduce blood flow to the rumen, ruminal motility, rumination (De *et al.*, 2017a) and appetite (Silanikove, 1992). There is also a decrease in foraging behaviour, which leads to significant water and ion losses in ruminants (Beede and Collier, 1986). The decreased feeding (Caroprese *et al.*, 2008) along with an increase in water consumption is a classic HS response observed in sheep as well (De *et al.*, 2020b). Sheep also increase the time spent near water (Caroprese *et al.*, 2008; Thomas *et al.*, 2008), adjust body posture and orientation towards the sun, increase standing (Bligh, 1985), and stay close to drinking water, thus reducing activity and conserving energy (Thomas *et al.*, 2008). Whenever water is available, they consume large amount of water in a single bout during summer (Naqvi *et al.*, 2013).

Standing and lying behaviour

The standing and lying behaviour of sheep changes with the change in temperature-humidity index (De *et al.*, 2017a; Li *et al.*, 2018). Lying down improves individual comfort and may reduce energy consumption

under high-temperature environments. Moreover, lying down may help to reduce heat load by transferring it to the floor, as floor is better conductive than air (Silanikove, 2000). However, sheep without shade conditions usually spend less time lying down as compared to animals which have access to shade (Lowe *et al.*, 2002; De *et al.*, 2020d). Increased standing could be a strategy to allow for more airflow and, therefore, convective cooling around the body (De *et al.*, 2020d). Sheep often form small, tight groups and position their heads beneath the bellies of other sheep to seek shade created by the bodies of their companions (Scott and Sutherland, 1981; Gregory, 1995).

Reproductive behaviour

Another adaptive behaviour of sheep in semi-arid regions is the timing of reproduction. They typically give birth during the most favourable times, when food availability and climate conditions are conducive to the year to enhance the survival of their offspring. In arid and semi-arid regions, where fluctuations in daylight, food, and water availability are substantial, the breeding season typically occurs from June to November. Consequently, kidding and lambing mainly happens between February and April (De *et al.*, 2016; De *et al.*, 2020a), when the conditions for new-borns are more favourable due to better food availability and improved climate (Jaber *et al.*, 2013; Naqvi *et al.*, 2013).

Conclusion

Thermal stress is apparent and causes substantial effects in hot, arid, and semi-arid regions, especially in the current climatic change scenarios. In this region, sheep husbandry is a sustainable livelihood option for the rural population. Moreover, the sheep of this region encounter multiple stresses comprising of nutritional stress, water stress and walking stress along with thermal stress. However, they have the capacity to adapt to such adverse extreme weather conditions through behavioural, morphological, physiological and genetic adaptation. Sheep generally modify their behaviour in terms of feeding, drinking, lying, shade seeking, rumination etc. Their morphological adaptation includes hair and wool characteristics, skin and coat colours, body shape and size and fat storage. Furthermore, many of the managerial modifications like the provision of shelter (De *et al.*, 2017d; De *et al.*, 2017e; De *et al.*, 2018), shade (De *et al.*, 2020d), cold water (De *et al.*, 2020b), desert cooler (De *et al.*, 2020c) can be followed to support the animal in ameliorating the HS effect. Further research on physical and behavioural adaptations is needed to understand and enhance sheep sustainability under changing climatic conditions.

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Author's contribution: KD: Conceptualization, writing-original draft, visualization, review and editing; JM: Writing- original draft; JB: Writing- original draft,

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