



SENSITIVITY, IMPACT AND CONSEQUENCES OF CHANGES IN RESPIRATORY RATE DURING THERMOREGULATION IN LIVESTOCK – A REVIEW

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Abstract

This review discusses the thermal conservative and heat dissipating roles of one of the most sensitive thermoregulatory variables (respiratory rate) with the aim of enhancing its application in evaluating both cold and heat adaptation. During cold exposure, livestock enhance the economy of body heat through reduction in respiratory rate with the extent of reduction being greater and commencing at relatively higher ambient temperature in poorly adapted phenotypes. This is accompanied by an increase in tidal volume and alveolar oxygen uptake, but a decrease in partial pressure of oxygen. On the other hand, heat stress induces increase in respiratory rate to enhance evaporative heat loss with the magnitude of such increase being greater and commencing at relatively lower ambient temperature in phenotypes that are poorly-adapted to heat. This is accompanied by a decrease in tidal volume and the development of hypocapnia. The increase in respiratory rate is observed to be greater, moderate and lesser in livestock that are mainly (pigs, rabbits and poultry), moderately (sheep, goats and *Bos taurus*) and less (*Zebu* cattle) dependent on respiratory evaporative heat loss, respectively. The changes during chronic heat stress may cause acid-base crisis in all livestock, in addition to reduction in eggshell quality in birds; due to marked decrease in partial pressure of carbon dioxide and a compensatory increase in elimination of bicarbonate. Within and between breed variations in sensitivity of respiratory rhythm to both cold and heat stress has shown high applicability in identifying phenotypes that are more susceptible to thermal stress; with some cellular and metabolic changes occurring to protect the animal from the consequences of hypo- or hyper-thermia. The information in this review may provide basis for identification of genes that support or suppress thermoregulation and may also be of great use in animal breeding, genomics and selective thermal stress mitigation to provide maximum protection and comfort to poorly-adapted phenotypes.

Key words: respiratory rate, thermoregulation, heat stress, poor adaptation, cold exposure

Experimentally, clinically and on farm, the thermoregulatory variable that can be measured with accuracy and ease by physical observation without any physiological recording device in livestock is respiratory rate. This rhythm is controlled by a centre

in the medulla oblongata and pons of the brainstem. Basically, three centres contribute to respiratory regulation, of which two (dorsal and ventral respiratory centres) are found in the medulla and one (pneumotaxic centre) in the pons (Coleman, 2011; Jerath et al., 2014). The most important centre (dorsal respiratory centre) is mainly responsible for inspiration, the ventral centre is responsible for both expiration and inspiration, and the pneumotaxic centre is involved in the control of breathing rate and pattern (Coleman, 2011). The dorsal respiratory centre is located within the nucleus solitarius where vagal and glossopharyngeal nerve fibres terminate and carry signals from peripheral chemoreceptors and baroreceptors (including the carotid and aortic bodies) and several lung receptors (Coleman, 2011; Spyer and Gourine, 2009). The centres control the rate and depth of respiration through various inputs in the form of neuronal signals, chemicals and hormones, with the ultimate aim of regulating the availability of oxygen and carbon dioxide, and supporting thermoregulation, especially in livestock (Pocock and Richards, 2006; Dzenda et al., 2015; Leite et al., 2018). Thus, activation of the respiratory centre during thermal stress is an important line of homeostatic defence by enhancing thermal conservation and dissipation during cold and heat stress, respectively. This is of great importance as variation in thermal environment due to seasonal changes affects all livestock and represents the largest single stressor in livestock production with significant negative impact on all aspects of production, including performance, reproduction and immunity (Habibu et al., 2016; Collier et al., 2017). Currently, the growing global interest is on the identification of improved methods of heat stress detection in order to enhance its management (Collier et al., 2017).

Over the years, the cardinal physiological or thermoregulatory variables (core body and skin temperatures, respiratory, sweating and pulse or heart rates) have been very reliable in evaluating the adaptive physiology of livestock with several techniques developed to maximise the information that could be obtained from these variables (Shultz, 1984; Jian et al., 2015; Dalcin et al., 2016; Minka and Ayo, 2016). Whereas, rectal temperature indicates the direct thermal state of an animal, the other thermoregulatory variables (skin temperature, respiratory, sweating, pulse and heart rate) reflect the thermolytic state of the animal (Kabuga, 1992; Jian et al., 2015; Habibu et al., 2017 a). Respiratory rate has been described as the most sensitive cardinal physiological variable to heat stress; and also as one of the most useful animal-based indicators of heat stress in livestock (Berman et al., 1985; Gaughan et al., 2000; Yaqub et al., 2017), as changes in respiratory rate always precede changes in other cardinal physiological variables (rectal temperature, sweating and pulse or heart rate) during heat stress (Jian et al., 2015; Dalcin et al., 2016; Singh et al., 2016). As such, it was suggested that changes in respiratory rate could be used as an on-farm animal welfare assessment tool to identify and classify animals into those that are susceptible or tolerant to heat or cold stress (Habibu et al., 2016; Rout et al., 2017). Such information could be useful in animal breeding, genomics and other manipulative techniques aimed at reducing the seasonal change-related mortality in livestock, and thus, improve productivity. The aim of this review is to discuss the available information on the role of respiratory rhythmicity in thermoregulation and the consequences of the rhythm during thermal stress in livestock with the view of

enhancing its application in identification, evaluation and measurement of both heat and cold stress and in selecting breeds that are more thermo-tolerant.

Ventilation versus thermoregulation

Depending on whether the body is in dire need to maintain blood gases or thermoregulate, a change in alveolar ventilation is accomplished by some breathing strategies such as increasing or decreasing respiratory rate, tidal volume and/or respiratory dead space (Gagliardi et al., 1997). Within the thermoneutral zone, ventilation is the main event, while thermoregulation remains quiescent until the respiratory centre is activated for thermal adjustment during cold or heat stress. During cold, respiratory rate and dead space ventilation decrease, while tidal volume increases (Diesel et al., 1985; Robertshaw, 2006). The expected decrease in alveolar ventilation due to reduced respiratory rate is checked by decrease in respiratory dead space and increase in tidal volume. During heat exposure, on the other hand, both 'thermolytic alveolar normo-ventilation' and 'thermolytic alveolar hyper-ventilation' have been reported (Gaughan et al., 2000). The most common change in all livestock exposed to heat stress is 'thermolytic alveolar normo-ventilation', in which an increase in respiratory rate and dead space, but a decrease in tidal volume occurs. Cattle, when exposed to severe heat stress that is not efficiently combated by respiratory evaporative heat loss (through rapid open mouth panting), may adopt 'thermolytic alveolar hyper-ventilation' where there is a relative decrease in respiratory rate (through deep open mouth panting), but an increase in tidal volume (Gaughan et al., 2000; Robertshaw, 2006).

Thermo-conservative role of respiratory rhythmicity

Adaptation to cold environments plays an important role in the survival of every animal, including tropical livestock which are poorly adapted to cold and are only exposed to lower grade of cold stress (10–12°C), especially those inhabiting the West African region affected by the cold-dry, dust-laden and windy harmattan season (Habibu et al., 2017 a; Minka and Ayo, 2014). At various degrees, tropical and sub-tropical livestock are exposed to cold depending on their geographical location. When livestock are exposed to cold environments, the sympathetic nervous system is activated causing vasoconstriction to reduce body heat loss. However, the degree to which the thermal environment can be adjusted internally by vasoconstriction is limited, and thus, thermogenesis mediated by endocrine signals and other more efficient mechanisms of reduction in heat loss must be activated to maintain optimal body temperature (Robertshaw, 2006; Collier et al., 2017).

Changes in respiratory rhythmicity also play a role in thermogenesis and the economy of body heat in livestock during cold stress. Through stimulation of thermoreceptors in the respiratory tract, exposure to low ambient temperature decreases the frequency of respiratory rhythmicity so as to reduce heat loss to the inhaled cold air (Diesel et al., 1985; Habibu et al., 2017 a). Even at such reduced frequency, respiratory heat loss is largely uncontrolled with the loss being countered by elevations in both metabolism and respiratory ventilation so as to maintain thermal homeostasis (Robertshaw, 2006). The reduction in respiratory rate is directly proportional to the

level of adaptation in most livestock; as sheep and goats that are adapted to cold show reduction in the magnitude of the decrease in respiratory rate and maintain higher body temperature, when compared with the poorly adapted sheep and goats during winter (Srikandakumar et al., 2003; Banerjee et al., 2014). Thus, the use of respiratory rate to evaluate the adaptation of goats to cold stress using multivariate analysis resulted in the classification of goats, distinctly into cold-susceptible (respiratory rate of < 24 breaths per minute) and cold-tolerant (respiratory rate of > 24 breaths per minute) phenotypes. This is unlike the use of respiratory rate to classify goats into heat susceptible and tolerant phenotypes. In addition, the cold-tolerant phenotypes had higher body temperature during the cold-dry season when compared with the cold-susceptible phenotypes, apparently due to the inability of the latter to increase circulating thyroid hormone concentrations beyond that of the former (Habibu et al., 2016). This suggests that among tropical breeds of goat (Red Sokoto and Sahel), some cold susceptible individuals do have lower respiratory rate and could easily develop hypothermia. The high respiratory rate in cold-adapted livestock may explain the higher partial pressure of oxygen observed in cold-adapted sheep compared with the poorly adapted ones, during winter and may also justify the higher rectal temperature in the former (Srikandakumar et al., 2003).

Unlike the high respiratory rate that causes increase in blood partial pressure of oxygen due to hyperventilation during heat stress, the low respiratory rate during cold exposure causes a decrease in partial pressure of oxygen (Srikandakumar et al., 2003; Sivakumar et al., 2010; Aarif and Aggarwal, 2016). The maintenance of high blood partial pressure of oxygen in cold-adapted breeds during winter may be an adaptive measure to increase oxygen availability for shivering and non-shivering thermogenesis (Srikandakumar et al., 2003). This is in order to increase metabolic rate and maintain body temperature above that of breeds that are poorly adapted to cold, especially the heat-adapted tropical livestock. In humans, oxygen intake has been shown to increase during winter when compared to summer (Nishimura et al., 2015). Both shivering and non-shivering thermogenesis are adapted by tropical breeds of livestock to prevent hypothermia in extreme cold conditions (Igono et al., 1982; Carstens, 1994). Thus, the major challenge of tropical livestock during cold exposure is to choose between maintaining higher respiratory rate so as to sustain higher oxygen availability and supplement respiratory heat loss by increasing metabolic heat production or reduce respiratory rate with subsequent decrease in oxygen availability but with reduction in the compromising effect of ambient temperature. Future studies need to examine the effects of reduced respiratory rate during cold stress on cellular respiration and thermogenesis as well as comparatively evaluate the variation in respiratory heat loss and thermogenic support in the following groups of livestock: (i) smaller livestock such as rabbits, which naturally have higher respiratory rate due to smaller body size (Gagliardi et al., 1997); (ii) livestock that depend mainly on respiratory rate for thermolysis (e.g. sheep and goats) and (iii) livestock that depend mainly on sweating for thermolysis (e.g. Zebu cattle). This will undoubtedly improve our understanding and management of cold stress in different species of livestock, especially in heat adapted livestock.

Thermolytic effect of respiratory rhythmicity during heat stress

As ambient temperature rises beyond the body temperature of mammals, thermoregulation is enhanced through cutaneous and respiratory evaporative cooling (Lara and Rostagn, 2013). With continuous rise in core body temperature due to high ambient thermal load, small ruminants and poultry, most especially sheep and broiler chickens, adopt panting to enhance the efficiency of heat dissipation. During panting, there is a controlled elevation in respiratory rate, but a decrease in tidal volume in order to increase ventilation of the upper respiratory tract, thus enhancing evaporative heat loss (Ingram and Legge, 1969; Robertshaw, 2006). Most heat exchange takes place at the nasal epithelial lining with the venous drainage being directed to a special network of arteries at the base of the brain where counter-current heat transfer takes place, so as to facilitate selective brain cooling and enhance the mechanism of thermal homeostasis (Du Preez, 2000; Robertshaw, 2006). To invest enough time and energy in reducing internal heat, heat-stressed animals become engrossed in increasing respiratory rate or panting, such that feed intake is reduced, causing reduction in body weight gain or loss of body weight. This ultimately diminishes the body energy available for reproduction and consequently leads to low productivity (Sejian et al., 2018).

With increase in respiratory rate, heat loss becomes faster, but with the negative consequences of dehydration. In extreme cases, the dehydration may slow down thermoregulation and reduce blood supply to the gut and gravid uterus (Habibu et al., 2018). Although other factors such as morphology of the skin and sweat glands, and type and conditions of the skin coat may influence the thermoregulatory body fluid economy of livestock leading to decrease or increase in erythrocyte parameters, rhythmicity of respiration appears to have greater impact especially in small ruminants (Pereira et al., 2008; Jian et al., 2014; Habibu et al., 2018). For instance, an episode of high respiratory rate in Sahel goats was accompanied by greater reduction in plasma volume (indicated by increase in PCV and RBC) when compared with the Red Sokoto goats that had lower respiratory rate (Habibu et al., 2017 a, b). This is likely associated with the greater dependence of small ruminants on heat loss through the respiratory tract than the skin (King, 1983; Silanikove, 2000). Generally, livestock show variation in their dependency on the means of evaporative heat loss during extreme heat stress. All livestock, to different extents, depend on the respiratory tract as means of evaporative heat loss during extreme heat stress; with pigs, rabbits and birds relying mainly on the respiratory tract for evaporative heat loss. This is due to the absence of sweat glands in birds and high number of non-functional sweat glands in pigs and rabbits (Marai et al., 2002; Huynh et al., 2005; Lara and Rostagn, 2013). This explains the need for high level of panting and poor tolerance to heat stress in these livestock. In pigs, the panting is not enough to efficiently dissipate heat and is supported by sensible heat loss through conduction, convection and radiation (Justino et al., 2014). In Morada Nova sheep that were more thermally stressed, the efficiency of cutaneous evaporative heat loss decreased, while that of respiratory evaporative heat loss increased with elevation in ambient thermal load (Silva et al., 2017; Leite et al., 2018). This was such that sweating rate progressively decreased with rise in ambient thermal load during the daytime despite

increase in skin temperature, while respiratory rate progressively increased (Silva et al., 2017). In goats, however, the efficiency of both cutaneous and respiratory evaporative losses increased with rise in ambient thermal load (Maia et al., 2015). It is, therefore, logical to infer that livestock that lack sweat gland or those with inherently less sweating ability and those in which sweating ability reduces as ambient thermal load increase, tend to pant during heat stress.

The heavy dependence of most livestock (except tropical large ruminants and other Zebu breeds of cattle) on respiratory evaporative heat loss and the promptness with which they resort to its use during moderate to severe heat stress explains the sensitivity of respiratory rate to high temperature-humidity index (Jian et al., 2015; Dalcin et al., 2016; Rout et al., 2017). In breeds of small ruminants with multiple coat colour, exposure to high thermal load increased the respiratory rate of goats and sheep with more pronounced rhythm in red and black coat animals when compared with others (white or brown coat animals; Srikandakumar et al., 2003; Maia et al., 2015; Leite et al., 2018). Similarly, age may influence the changes in respiratory rate during heat stress. Due to thermoregulatory immaturity, weaned ewe-lambs had an increase in rectal temperature and respiratory rate when compared with older ewes in the afternoon when heat load increased (Thwaites, 1967; Macias-Cruz et al., 2018). Hence, the use of variation in respiratory rate to classify goats into heat stress-susceptible (those with higher respiratory rate) and heat stress-tolerant (those with lower respiratory rate) phenotypes indicated higher rectal temperature and heat shock proteins (Rout et al., 2017), but lower triiodothyronine (Habibu et al., 2016) in heat stress-susceptible than heat stress-tolerant phenotypes. This change suggests that the population of goats that are more susceptible to heat stress need to evolve more efficient mechanisms to check cellular damage and reduce metabolic heat production in order to alleviate the effect of high body temperature induced by elevated environment temperature.

On the other hand, the use of respiratory rate to detect susceptibility or tolerance to heat stress in Zebu cattle is applicable, but may not be as sensitive as in small ruminants due to the former's greater dependence on sweating as a means of critical evaporative heat loss (King, 1983; Jian et al., 2015). In Zebu cattle, about 84% of body heat is lost by evaporation, of which 65% is by sweating and 35% by panting (McLean and Calvert, 1972; de Souza et al., 2018). The classification of Zebu breed of cattle (Nellore) according to their capacity to dissipate body heat as 'efficient' or 'inefficient' showed that sweating was the thermoregulatory parameter, particularly responsible for the lower rectal temperature in the Nellore cows that were efficient in heat dissipation, while respiratory rate did not significantly vary between the groups of cattle that were 'efficient' and those that were 'inefficient' in heat dissipation (Hooper et al., 2018). Thus, suggesting that sweating, but not respiratory rate gives an edge in heat tolerance of Zebu cattle. During heat stress, there is increase in respiratory rate and sweating rate in both *Bos indicus* and *Bos taurus*. In *Bos taurus*, however, cutaneous evaporative heat loss becomes less efficient as ambient heat load continue to increase. This is because the mechanism of sweating is limited and attains a plateau with rise in ambient heat load due to morphometric features that do not support continuous production of sweat for evaporative heat loss (Jian et

al., 2014; 2015). Both *Bos indicus* and *Bos taurus* have apocrine sweat glands with the same perimeter (Carvalho et al., 1995; Collier et al., 2008). However, the glands of *Bos taurus* are less baggy-shaped, have lower density and are poorly active (Nay and Heyman, 1956; Jian et al., 2014; de Souza et al., 2018). Thus, Holstein Friesian cattle and their crossbreeds with higher genetic factions usually resort to the use of respiratory evaporative heat loss heavily and promptly like small ruminants during heat stress (Jian et al., 2015). Therefore, variation in respiratory rate of these breeds may be applicable in the identification of phenotypes that are susceptible or tolerant to heat stress. However, another challenge with the use of respiratory rate to identify phenotypes that are susceptible or tolerant to heat stress is the decrease in respiratory rate in cattle exposed to heat stress (Ingram and Legge, 1969; Gaughan et al., 2000), due mainly to a change from rapid, shallow open-mouth panting to deep slow close-mouth panting (Gaughan et al., 2000; Beatty et al., 2006).

Of all the thermoregulatory variables, the upper critical or inflection point temperature/temperature-humidity index (THI) of respiratory rate is usually the first to be reached during exposure to high ambient temperature so as to activate the mechanisms of heat loss through respiratory evaporative heat loss and convection (Gaughan et al., 2000; Huynh et al., 2005; Dalcin et al., 2016). The effect of the upper critical limit of ambient heat load on respiratory rate is reached at intervals that vary with the species of livestock exposed to heat stress. This is because the heat-induced change in respiratory rate lags behind increase in ambient heat load and, thus, livestock, especially cattle, should be exposed long enough for respiratory thermoregulation to be activated before the variation in respiratory rate could be used to identify adapted phenotypes (Gaughan et al., 2000).

Effect of heat stress-induced increase in respiratory rate on acid-base balance

The dual functions of the respiratory system in controlling both blood gas tension and thermoregulation is expected to represent a potential homeostatic conflict during heat stress due to the role of hypocapnia in suppressing respiratory rhythm and that of hyperthermia in stimulating respiratory rhythm (Entin et al., 2005). However, increase in body temperature has been shown to be the most important factor controlling respiratory rate during heat stress as the expected suppressive effect of hypocapnia is “turned off” (Entin et al., 2005; Robertshaw, 2006). Thus, high respiratory rate is maintained during heat stress in spite of hypocapnia.

Animals with small body size and relatively higher heat production and absorption usually pant more than they sweat. For instance, most breeds of sheep and goats pant more than they sweat, while most breeds of cattle and camels sweat more than they pant (King, 1983). Although sheep may experience very fast open-mouth panting during heat stress, the extent of the increase in core temperature and reduction in blood carbon dioxide tension is less in sheep compared to cattle. This observation may indicate a different degree of dead space ventilation in sheep, where very rapid shallow panting does not result in blowing off of carbon dioxide to the extent to which it occurs in cattle (Barnes et al., 2004). The ease with which high respiratory rate reduces blood carbon dioxide tension in cattle may contribute to the reasons

they prefer evaporative heat loss through sweating than panting. Even among small ruminants, the thermoregulatory efficiency of panting is higher in sheep, which have been shown to rely more on panting for evaporative cooling than goats (King, 1983). Through respiratory evaporative water loss mainly, sheep can more efficiently minimise the increase in body temperature during heat stress compared to goats, which rely more on cutaneous evaporative water loss (Rahardja et al., 2011). Due to a number of reasons which have been outlined by King (1983), panting seems to be a more efficient method of evaporative cooling than sweating. Firstly, though both methods rely on heat loss via latent heat of evaporation from the body core (Silanikove, 2000; Luz et al., 2016), sweating can also utilise the energy of solar radiation on the skin, thus minimising the amount of heat loss by the body during heat stress. Secondly, panting also provides its own airflow (which is different from the prevailing environmental conditions) over moist surfaces, thus facilitating evaporation. Thirdly, there is no loss of salt and electrolytes in panting, as in sweating; except if there is dripping of saliva out of the mouth (King, 1983). Finally, panting may help to cool the brain even when the body temperature is rising. By cooling the nasal and oral passages, the blood that flows into the venous sinus, bathing the carotid plexus is cooled, thus the blood supply to the brain is cooled (Taylor and Lyman, 1972).

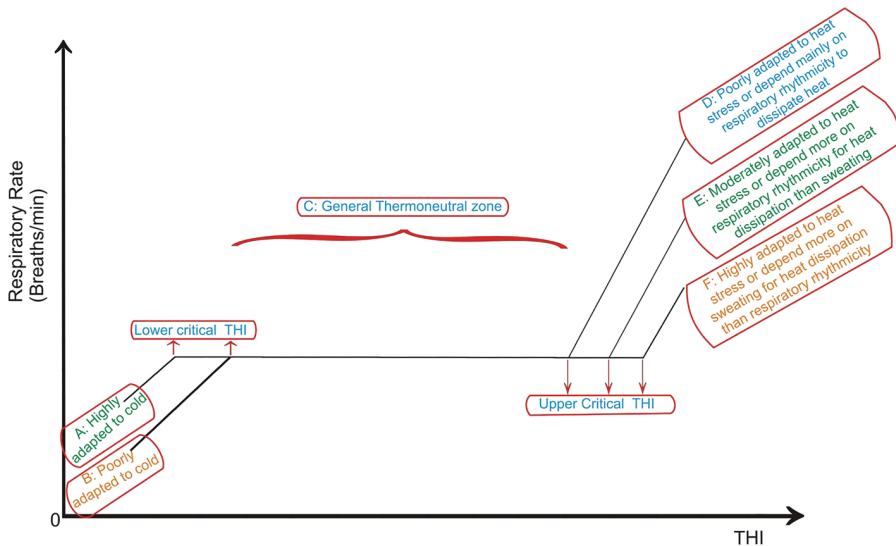


Figure 1. Dynamics of respiratory rate with changes in temperature-humidity index (THI). At the lower critical THI (Arieli et al., 1980), 'A' represents the decrease in respiratory rate of livestock that are highly adapted to cold stress as they can maintain normal range of respiratory rate ('C') at low THI when compared with livestock in line 'B' which are poorly adapted to cold stress. At the upper critical THI (Huynh et al., 2005), 'D' represents the increase in respiratory rate of livestock that are poorly adapted to heat stress or depend mainly on respiratory evaporative heat loss (e.g., pigs, rabbits and poultry) during heat stress. While the second increase in respiratory rate ('E') denotes livestock that are moderately adapted to heat stress or depend more on respiratory than cutaneous evaporative heat loss (e.g., sheep, goats and Holstein-Friesian cattle) during heat stress. The terminal increase in respiratory rate ('F') denotes livestock that are highly adapted to heat stress or depend more on cutaneous than respiratory evaporative heat loss (Zebu cattle) during heat stress

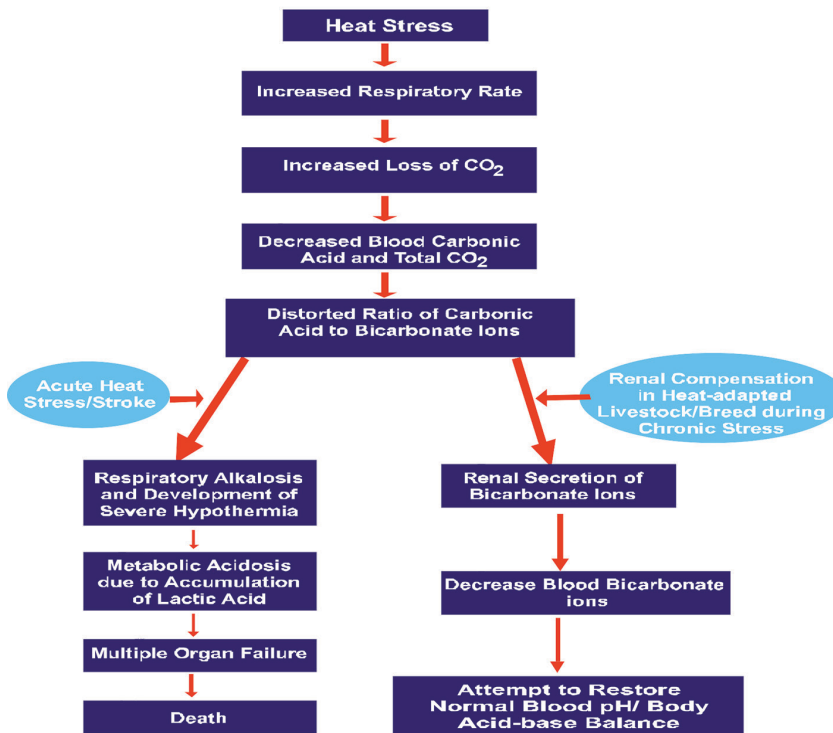


Figure 2. Physiological changes and renal adjustments in acid-base balance in livestock during heat stress

The disadvantages of panting include a risk of respiratory alkalosis due to the decrease in partial pressure of carbon dioxide in the blood (Figure 2), and increased activity of the respiratory muscles, which may add to the excess heat load (Aarif and Aggarwal, 2016; Luz et al., 2016). However, the unique property of the respiratory system enables it to own a natural rhythm that could mitigate this risk (King, 1983). Heat stress-induced hyperventilation is responsible for the increase in blood pH due to decrease in partial pressure of carbon dioxide, total carbon dioxide (TCO₂), concentration of bicarbonate, base excess in blood (BE_b) and extracellular fluid (BE_{ecf}) in goats (Hamzaoui et al., 2013), sheep, cattle (Barnes et al., 2004), buffaloes (Aarif and Aggarwal, 2016), pigs (Cottrell et al., 2017) and ducks (Park and Kim, 2016; Park and Park, 2017) with the magnitude of the change being less in the heat-adapted *Bos indicus* and Awassi sheep (Barnes et al., 2004). This finding indicates that the heat-adapted sheep and cattle were able to compensate for the tendency towards respiratory alkalosis and minimise the increase in blood pH (Figure 2). The decrease in concentration of bicarbonate has been shown to result from a compensatory renal response that increases the excretion of bicarbonate to maintain the standard ratio of plasma bicarbonate to PCO₂ (20:1; Masero and Siegel, 1977; Aarif and Aggarwal, 2016). Unlike in Awassi and Merino sheep, the rapid increase in blood carbon

dioxide tension after cessation of heat stress in *Bos taurus* and *Bos indicus* was not matched by an increase in blood bicarbonate concentrations, leading to acidosis, with a resultant reduction in blood and urine pH (Beatty et al., 2006). Thus, it was hypothesised that post-exposure to heat stress, the changes in the body's buffering capacity may further compromise the health status of cattle by predisposing them to alteration in acid-base balance, such as feed-related metabolic acidosis (Barnes et al., 2004). In sheep exposed to different seasons of the year, the elevation in respiratory rate during heat stress caused a decrease in partial pressure of carbon dioxide, which was accompanied by increase in blood pH during the hot season in comparison with the cold season. This may be due to weak renal compensation as an increase in concentration of bicarbonate was recorded during the hot season in comparison with the cold season (Srikandakumar et al., 2003). Heat stress-induced respiratory alkalosis in birds may reduce blood bicarbonate and carbonic acid, thereby, lowering the availability of carbonate required for eggshell formation (Taylor, 1970). This, in conjunction with reduction in the production of calcium-binding protein (calbindin) in the intestine and eggshell gland, is mainly responsible for the degradation in eggshell quality during heat stress (Marder and Arad, 1989; Ebeid et al., 2012).

The duration and magnitude of heat exposure may influence the changes in acid-base balance in mammals. Unlike chronic heat stress (induced by seasonal/diurnal heat stress) which causes respiratory alkalosis in livestock, acute heat stress/stroke have been shown to cause both respiratory alkalosis and metabolic acidosis in goats, dog heat stroke model and humans, with metabolic acidosis predominating, particularly when the duration of the acute heat exposure is prolonged (Magazanik et al., 1980; Bouchama and De Vol, 2001; Temizel et al., 2009). During such exposure, metabolic acidosis caused by lactic acid may be observed at a certain body temperature threshold (Magazanik et al., 1980) with the risk of multiple organ failure associated with neurological morbidity and mortality (Bouchama and De Vol, 2001). In Saanen goat kids accidentally exposed to heat stroke, rectal temperature rose to a mean value of 41.8°C (41.4–42.1°C) and circulating lactate markedly increased, with death in the kids that had higher circulating lactate concentration (Temizel et al., 2009). Clues have been proposed with respect to the cause of increase in production of lactic acid during acute heat stress, including: anaerobic metabolism due to hyperthermia-induced sudden reduction in oxygen uptake (Magazanik et al., 1980); and starvation of skeletal muscles due to heat-induced dehydration as a result of redirection of blood flow to visceral organs (Temizel et al., 2009; Kraut and Madias, 2014).

Conclusion

As seasons change, respiration is adjusted to equilibrate ventilation and thermoregulation through decrease in respiratory rate, but increase in tidal volume during cold exposure and increase in respiratory rate, but decrease in tidal volume during heat exposure. These changes ensure that thermoregulation is adjusted to reduce heat loss during cold exposure and enhance heat loss during heat exposure; while, ventilation is adjusted using tidal volume. In most livestock, greater magnitude of reduction in respiratory rate during cold exposure is suggestive of poor adaptation to cold stress, while higher magnitude of increase in respiratory rate during exposure

to high environmental temperature is suggestive of poor adaptation to heat stress. Thus, changes in respiratory rate can be adopted in identifying livestock phenotypes that are poorly or highly adapted to thermal stress. The main negative consequences of changes in respiratory rate are dehydration and respiratory alkalosis. Chronic heat stress, which is the common form of heat stress tropical livestock have to contend with, may cause respiratory alkalosis. Expectedly, this acid-base challenge is checked by renal compensatory loss of bicarbonate ions, with greater magnitude in highly adapted livestock. On the other hand, exposure to acute heat stress/stroke may cause both respiratory alkalosis and metabolic acidosis with metabolic acidosis caused by increased production of lactic acid predominating, particularly when the duration of the acute heat exposure is prolonged. Thus, management of acute heat stress should be geared towards reducing the accumulated systemic lactate levels.

Reference

- Aarif O., Aggarwal A. (2016). Dry period cooling ameliorates physiological variables and blood acid base balance, improving milk production in Murrah buffaloes. *Int. J. Biometeorol.*, 60: 465–473.
- Arieli A., Meltzer A., Berman A. (1980). The thermoneutral temperature zone and seasonal acclimatisation in the hen. *Brit. Poultry Sci.*, 21: 471–478.
- Banerjee D., Upadhyay R.C., Chaudhary U.B., Kumar R., Singh S., Ashutosh Das T.K., De S., (2014). Seasonal variations in physio-biochemical profiles of Indian goats in the paradigm of hot and cold climate. *Biol. Rhythm Res.*, 46: 221–236.
- Barnes A., Beatty D., Taylor E., Stockman C., Maloney S., McCarthy M. (2004). Physiology of heat stress in cattle and sheep. Meat and Livestock Australia, Project number LIVE.209, pp. 1–36.
- Beatty D.T., Barnes A., Taylor E., Pethick D., McCarthy M., Maloney S.K. (2006). Physiological responses of *Bos taurus* and *Bos indicus* cattle to prolonged, continuous heat and humidity. *J. Anim. Sci.*, 84: 972–985.
- Berman A., Folman Y., Kaim M., Mamen M., Herz Z., Wolfenson D., Arieli A., Graber Y. (1985). Upper critical temperatures and forced ventilation effects for high-yielding dairy cows in a subtropical environment. *J. Dairy Sci.*, 68: 1488–1495.
- Bouchama A., De Vol E.B. (2001). Acid-base alteration in heatstroke. *Intens. Care Med.*, 27: 680–685.
- Carstens G.E. (1994). Cold thermoregulation in the newborn calf. *Vet. Clin. North Am. Food Anim. Pract.*, 10: 69–106.
- Carvalho F.A., Lammoglia M.A., Simoes M.J., Randel R.D. (1995). Breed affects thermoregulation and epithelial morphology in imported and native cattle subjected to heat stress. *J. Anim. Sci.*, 73: 3570–3573.
- Coleman M.D. (2011). Respiratory and pulmonary physiology. In: Anesthesia secrets, Duke J., (ed). Elsevier Inc., <https://doi.org/10.1016/C2009-0-54968-9>.
- Collier R.J., Collier J.L., Rhoads R.P., Baumgard L.H. (2008). Invited review: genes involved in the bovine heat stress response. *J. Dairy Sci.*, 91: 445–454.
- Collier R.J., Renquist B.J., Xiao J.Y.A. (2017). 100-year review: Stress physiology including heat stress. *J. Dairy Sci.*, 100: 10367–10380.
- Cottrell J.J., Liu F., Wan S., Wijesiriwardana U.A., DiGiacomo K., Kelly F., Celi P., Leury B., Clarke I.J., Dunshea F.R. (2017). The effect of heat stress on respiratory alkalosis, blood acid base balance and insulin sensitivity in cinnamon supplemented pigs. *Anim. Prod. Sci.*, 57: 2415–2415.

- Dalcin V.C., Fischer V., Daltro D.S., Alfonzo E.P.M., Stumpf M.T., Kolling G.J., da Silva M.V., McManus C. (2016). Physiological parameters for thermal stress in dairy cattle. *R. Bras. Zootec.*, 45: 458–465.
- Diesel D.A., Tucker A., Robertshaw D. (1985). Cold-induced changes in breathing pattern as a strategy to reduce respiratory heat loss. *J. Appl. Physiol.*, 69: 1946–1952.
- Du Preez J.H. (2000). Parameters for the determination and evaluation of heat stress in dairy cattle in South Africa. *Onderstepoort J. Vet. Res.*, 67: 263–271.
- Dzenda T., Ayo J.O., Lakpini C.A.M., Adelaiye A.A. (2015). Diurnal, seasonal and sex influences on respiratory rate of African Giant rats (*Cricetomys gambianus*, Waterhouse) in a tropical Savannah. *Wulfenia J.*, 22: 475–485.
- Ebeid T.A., Suzuki T., Sugiyama T. (2012). High ambient temperature influences eggshell quality and calbindin-D28k localization of eggshell gland and all intestinal segments of laying hens. *Poultry Sci.*, 91: 2282–2287.
- Entin P.L., Robertshaw D., Rawson R.E. (2005). Reduction of the Pa_{CO_2} set point during hyperthermic exercise in the sheep. *Comp. Biochem. Physiol. A*, 140: 309–316.
- Gagliardi L., Rusconi F., Castagneto M., Porta G.L.N., Razon S., Pellegatta A. (1997). Respiratory rate and body mass in the first three years of life. *Arch. Dis. Child.*, 76: 151–154.
- Gaughan J.B., Holt S.M., Hahn G.L., Mader T.L., Eigenberg R. (2000). Respiration rate – is it a good measure of heat stress in cattle? *Asian Austral. J. Anim. Sci.*, 13: 329–332.
- Habibu B., Kawu M.U., Makun H.J., Aluwong T., Yaqub L.S. (2016). Seasonal variation in body mass index cardinal physiological variables and serum thyroid hormones profiles in relation to susceptibility to thermal stress in goats kids. *Small Rum. Res.*, 145: 20–27.
- Habibu B., Kawu M.U., Makum H.J., Aluwong T. (2017 a). Influence of seasonal changes on physiological variables, haematology and serum thyroid hormones profile in male Red Sokoto and Sahel goats. *J. Appl. Anim. Res.*, 45: 508–516.
- Habibu B., Kawu M., Makun H., Aluwong T., Yaqub L., Dzenda T., Hajarrah Buhari H. (2017 b). Influences of breed, sex and age on seasonal changes in haematological variables of tropical goat kids. *Arch. Anim. Breed.*, 60: 33–42.
- Habibu B., Dzenda T., Ayo J.O., Yaqub L.S., Kawu M.U. (2018). Haematological changes and plasma fluid dynamics in livestock during thermal stress, and response to mitigative measures. *Livest. Sci.*, 214: 189–201.
- Hamzaoui S., Salama A.A.K., Albanell E., Such X., Caja G. (2013). Physiological responses and lactational performances of late-lactation dairy goats under heat stress conditions. *J. Dairy Sci.*, 96: 1–11.
- Hooper H.B., Titto C.G., Gonella-Díaz A.M., Henriqu, F.L., Pulido-Rodríguez L.F., Longo A.L.S., Leme-dos-Santos T.M.C., Geraldo A.C.A.P.M., Pereira A.M.F., Binelli M., Balieiro J.C.C., Titto E.A.L. (2018). Heat loss efficiency and HSPs gene expression of Nellore cows in tropical climate conditions. *Inter. J. Biometeorol.*, doi: [10.1007/s00484-018-1576-5](https://doi.org/10.1007/s00484-018-1576-5)
- Huynh T.T.T., Aarnink A.J.A., Verstegen M.W.A., Gerrits W.J.J., Heetkamp M.J.W., Kemp B., Canh T.T. (2005). Effects of increasing temperatures on physiological changes in pigs at different relative humidities. *J. Anim. Sci.*, 83: 1385–1396.
- Igono M.O., Molokwu E.C.I., Aliu Y.O. (1982). Body temperature responses of Savanna Brown goat to the harmattan and hot-dry seasons. *Int. J. Biometeorol.*, 26: 225–230.
- Ingram D.L., Legge K.F. (1969). The effect of environmental temperature on respiratory ventilation in the pig. *Respir. Physiol.*, 8: 1–12.
- Jerath R., Crawford M.W., Barnes V.A., Kyler H. (2014). Widespread depolarization during expiration: a source of respiratory drive? *Med. Hypoth.*, 84: 31–37.
- Jian W., Ke Y., Cheng L. (2015). Physiological responses and lactation to cutaneous evaporative heat loss in *Bos indicus*, *Bos taurus*, and their crossbreds. *Asian Austral. J. Anim. Sci.*, 28: 1558.
- Jian W., Duangjinda M., Vajrabukka C., Katawatin S. (2014). Differences of skin morphology in *Bos indicus*, *Bos taurus*, and their crossbreds. *Int. J. Biometeorol.*, 58: 1087–1094.
- Justino E., Naas I.D.A., Carvalho T.M.R., Neves D.P., Salgado D.D. (2014). The impact of evaporative cooling on the thermoregulation and sensible heat loss of sows during farrowing. *Eng. Agr., Jaboticabal*, 34: 1050–1061.

- Kabuga J.D. (1992). The influence of thermal conditions on rectal temperature, respiration rate and pulse rate of lactating Holstein-Friesian cows in the humid tropics. *Int. J. Biometeorol.*, 36: 146–150.
- King J.M. (1983). Livestock water needs in pastoral Africa in relation to climate. *ILCA Res. Rep.*, 7: 1–95.
- Kraut J.A., Madias N.E. (2014). Lactic acidosis. *N. Engl. J. Med.*, 371: 2309–2319.
- Lara L.J., Rostagn M.H. (2013). Impact of heat stress on poultry production. *Animals*, 3: 356–369.
- Leite J.H.G.M., Da Silva R.G., Silva W.S.T., Silva W.E., Paiva R.D.M., Sousa J.E.R., Asensio L.A.B., Façanha D.A.E. (2018). Locally adapted Brazilian ewes with different coat colors maintain homeothermy during the year in an equatorial semiarid environment. *Inter. J. Biometeorol.*, 62: 1635–1644.
- Luz C.S.M., Fonseca W.J.L., Vogado G.M.S., Fonseca W.L., de Oliveira M.R.A., Sousa G.G.T., Farias L.A., de Sousa S.C. Jr (2016). Adaptive thermal traits in farm animals. *J. Anim. Behav. Biometeorol.*, 4: 6–11.
- Macías-Cruz U., Correa-Calderón A., Mellado M., Meza-Herrera C.A., Aréchiga C.F., Avendaño-Reyes L. (2018). Thermoregulatory response to outdoor heat stress of hair sheep females at different physiological state. *Int. J. Biometeorol.*, <https://doi.org/10.1007/s00484-018-1615-2>.
- Magazani A., Shapiro Y., Shibolet S. (1980). Dynamic changes in acid base balance during heatstroke in dogs. *Pflügers Arch.*, 388: 129–135.
- Maia A.S.C., Da Silva R.G., Nascimento S.T., Nascimento C.C.N., Pedrosa H.P., Domingos H.G.T. (2015). Thermoregulatory responses of goats in hot environments. *Int. J. Biometeorol.*, 59: 1025–1033.
- Marai I.F.M., Habeebb A.A.M., Gad A.E. (2002). Rabbits' productive, reproductive and physiological performance traits as affected by heat stress: a review. *Livest. Prod. Sci.*, 78: 71–90.
- Marder J., Arad Z. (1989). Panting and acid-base regulation in heat stressed birds. *Comp. Biochem. Physiol. A Comp. Physiol.*, 94: 395–400.
- Masero E.J., Siegel P.D. (1977). Acid base regulation, its physiology and pathology and interpretation of blood gas analysis. 2nd ed. W.B. Saunders, Philadelphia.
- McLean J.A., Calvert D.T. (1972). Influence of air humidity on the partition of heat exchange of cattle. *J. Agric. Sci.*, 78: 303–307.
- Minka N.S., Ayo J.O. (2014). Influence of cold-dry (harmattan) season on colonic temperature and the development of pulmonary hypertension in broiler chickens, and the modulating effect of ascorbic acid. *O. A. Anim. Physiol.*, 6: 1–11.
- Minka N.S., Ayo J.O. (2016). Effects of cold-dry (harmattan) and hot-dry seasons on daily rhythms of rectal and body surface temperatures in sheep and goats in a natural tropical environment. *J. Circadian Rhythms*, 14: 1–11.
- Nay T., Heyman R.H., (1956). Sweat glands in zebu (*Bos indicus* L.) and European (*B. taurus* L.) cattle. *Aust. J. Agric. Res.*, 7: 482–494.
- Nishimura T., Motoi M., Egashira Y., Choi D., Aoyagi K., Watanuki S. (2015). Seasonal variation of non-shivering thermogenesis (NST) during mild cold exposure. *J. Physiol. Anthropol.*, <http://dx.doi.org/10.1186/s40101-015-0051-9>.
- Park B.S., Park S.O. (2017). Effects of feeding time with betaine diet on growth performance, blood markers, and short chain fatty acids in meat ducks exposed to heat stress. *Livest. Sci.*, 199: 31–36.
- Park S.O., Kim W.K. (2016). Effects of betaine on biological functions in meat-type ducks exposed to heat stress. *Poultry Sci.*, 96: 1212–1218.
- Pereira A.M.F., Baccari F.J., Titto E.A.L., Almeida J.A.A. (2008). Effect of thermal stress on physiological parameters, feed intake and plasma thyroid hormones concentration in Alentejana, Mertolenga, Frisian and Limousine cattle breeds. *Int. J. Biometeorol.*, 52: 199–208.
- Poock G., Richards C.D. (2006). Human physiology: the basis of medicine. 3rd ed. Oxford: Oxford University Press, pp. 332–336.
- Rahardja D.P., Toleng A.L., Lectari V.S. (2011). Thermoregulation and water balance in fat-tailed sheep and Kacang goat under sunlight exposure and water restriction in a hot and dry area. *Animal*, 10: 1587–1593.

- Robertshaw D. (2006). Mechanisms for the control of respiratory evaporative heat loss in panting animals. *J. Appl. Physiol.*, 101: 664–668.
- Rout P.K., Kaushik R., Ramachandran N., Jindal S.K. (2017). Identification of heat stress-susceptible and -tolerant phenotypes in goats in semiarid tropics. *Anim. Prod. Sci.*, 58: 1349–1357.
- Sejian V., Bhatta R., Gaughan J.B., Dunshea F.R., Lacetera N. (2018). Review: Adaptation of animals to heat stress. *Animal*, 12: s431–s444.
- Shultz T.A. (1984). Weather and shade effects on corral cow activities. *J. Dairy Sci.*, 67: 868–873.
- Silanikove N. (2000). Effects of heat stress on the welfare of extensively managed domestic ruminants. *Livest. Prod. Sci.*, 67: 1–18.
- Silva W.E., Leite J.H.G.M., Souza J.E.R., Costa W.P., Silva W.S.T., Guilhermino M.M., Bermejo L.A., Façanha D.A.E. (2017). Daily rhythmicity of the thermoregulatory responses of locally adapted Brazilian sheep in a semiarid environment. *Int. J. Biometeorol.*, 61: 1221–1231.
- Singh K.M., Singh S., Ganguly I., Ganguly A., Nachiappan R.K., Chopra A., Narula H.K. (2016). Evaluation of Indian sheep breeds of arid zone under heat stress condition. *Small Rum. Res.*, 141: 113–117.
- Sivakumar A.V.N., Singh G., Varshney V.P. (2010). Antioxidants supplementation on acid base balance during heat stress in goats. *Asian Austral. J. Anim. Sci.*, 23: 1462–1468.
- Souza J.B.F. de, de Queiroza J.P.A.F., dos Santos V.J.S., Dantasb M.R.T., de Lima R.N., Limad P.O., Costa L.L.M. (2018). Cutaneous evaporative thermolysis and hair coat surface temperature of calves evaluated with the aid of a gas analyzer and infrared thermography. *Comp. Elect. Agric.*, 154: 222–226.
- Spyer K.M., Gourine A.V. (2009). Chemosensory pathways in the brainstem controlling cardiorespiratory activity. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 364: 2603–2610.
- Srikandakumar A., Johnson E.H., Mahgoub O. (2003). Effect of heat stress on respiratory rate, rectal temperature and blood chemistry in Omani and Australian Merino sheep. *Small Rum. Res.*, 49: 193–198.
- Taylor C.R., Lyman C.P. (1972). Heat storage in running antelopes: Independence of brain and body temperatures. *Am. J. Physiol.*, 221: 114–117.
- Taylor T.G. (1970). How an eggshell is made. *Sci. Amer.*, 222: 88–95.
- Temizel E.M., Senturk S., Kasap S. (2009). Clinical, haematological and biochemical findings in Saanen goat kids with naturally occurring heat stroke. *Tierärztliche Praxis Großtiere*, 37(G): 236–241.
- Thwaites C.J. (1967). Age and heat tolerance in sheep. *Int. J. Biometeorol.*, 11: 209–212.
- Yaqub L.S., Ayo J.O., Kawu M.U., Rekwot P.I. (2017). Diurnal thermoregulatory responses in pregnant Yankasa ewes to the dry season in a tropical Savannah. *Trop. Anim. Health Prod.*, 49: 1243–1252.

Received: 22 VI 2018

Accepted: 3 I 2019