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IMPACTS OF HEAT STRESS ON MEAT QUALITY AND STRATEGIES FOR AMELIORATION; A REVIEW

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ABSTRACT

During the summer, high ambient temperature and humidity cause economic loss to the global livestock industry via reduced livestock productivity and increased mortality. The problem of heat stress (HS) is likely to be exacerbated by global warming and climate change. Recent research has shown that HS not only leads to physiological and metabolic perturbations in live animals,but can also affect carcass and meat quality characteristics plausibly by altering the rate and extent of postmortem muscle glycolysis and resultant pH. However, these impacts of HS are not consistent across species. Higher incidence of pale soft and exudative (PSE) meat has been reported in poultry. On the contrary, higher incidence of high ultimate pH and dark firm and dry (DFD) meat or no impacts of HS have been reported in sheep and cattle. With the limited data on HS impacts on meat quality of ruminants, it is difficult to explain the exact mechanisms driving theses variable impacts. However, it is hypothesized that the severity and duration of HS may lead to variable impacts due to lack of opportunity to adapdate to acute heat exposure. Longer HS exposure may allow ruminants to adapdate to heat and may not record any negative impacts on meat quality. This paper reviews the recent research on impacts of HS on meat quality characteristics and identify the key areas of further research required to better understand these negative impacts to develop strategies for amelioration. In addition, some mitigation strategies of HS have also been discussed which include both managemental and nutritional interventions.

Key words: heat stress, meat quality, ruminants, monogastrics, feed additives.

ABBREVIATIONS

HS	**Heat stress**
TN	**Thermoneutral**
PSE	**Pale, soft, exudative**
DFD	**Dark firm and dry meat**
THI	**Temperature–humidity index**
RH	**Relative humidity**
RT	**Rectal temperature**
RR	**Respiration rate**
WHC	**Water holding capacity**
WBSF	**Warner–Bratzler shear force**
pHu	**Ultimate pH**
IMF	**Intramuscular fat**
LTL	**Longissimus thoracis et lumborum**
LL	**Longissimus lumborum**

1. INTRODUCTION

High ambient temperature compromises animal welfare and productivity due to heat stress (HS) experienced over summer months. Heat stress has become one of the major challenges facing global livestock production, especially in the warmer parts of the world (Bernabucci et al. 2010; Rhoads et al. 2013). Recent deaths of 2400 Australian sheep due to HS on a ship to the Middle East (https://www.theguardian.com/world/2018/apr/05/disgusting-death-of-2900-australian-sheep-on-ship-to-middle-east-sparks-investigation) has highlighted animal welfare issues and severe consequences of HS in sheep. It has also increased the vulnerability of Australian live livestock export business, which could lead to millions of dollar economic losses. According to meteorological data, Australia's yearly temperature was on average higher 1 to 1.5 °C from 1910 to 2018, (State of the Climate 2018, Australian Government Bureau of Meteorology). In Australia, during the years 2013-2017, there was a 27 per cent increase in the number of hot days above 35°C (Osei-Amponsah et al. 2019), and year 2019 was warmest year on record, with the annual national mean temperature 1.52 °C above average (BOM, 2019). The CMIP5 (Coupled Model Intercomparison Project phase 5) climate modelling projections indicated that the heat waves in Australia will become longer, more frequent and hotter by the end of 21st century (Cowan et al. 2014). It is predicted that the impacts of HS will be further exacerbated by climate change. As reviewed by others (Gregory 2010; Johnson 2018; Gonzalez et al. 2020), extremes in summertime temperatures impose negative effects on animal growth performance, alter carcass composition and increase the risk of pale, soft, exudative (PSE) or PSE-like meat in pigs, poultry and beef cattle, and dark firm and dry (DFD) meat in ruminants.

Therefore, a better understanding of HS impacts on animal welfare, production and product quality is required to develop suitable strategies to mitigate HS to promote animal welfare and sustainable production. This paper reviews the current knowledge and research progress of HS impacts on meat quality and identifies some of the potential nutritional interventions to alleviate the negative consequences of HS to improve meat quality.

2. HEAT STRESS

"Stress" is defined as the body's response to external forces, which tends to displace its system from the resting or basal state (Hancock 2006). Heat stress occurs when the ambient temperature is higher than the animal’s thermoneutral zone (TNZ, the range of environmental temperature within which the animals uses no additional energy to maintain their body temperature). The TNZ is influenced by many environmental factors which would affect heat gain and loss from an animal’s body such as wind velocity, air temperature, humidity, precipitation, solar radiation, animal breed and availability of shade or shelter (Bernabucci et al. 2010; Aggarwal and Upadhyay 2013).

2.1 ASSESSMENT OF HEAT STRESS SEVERITY

The temperature–humidity index (THI) is used to quantify HS and is calculated based on the environmental temperature combined with relative humidity (high humidity could reduce an animal’s evaporative cooling efficiency, thus affecting animal TNZ). The THI offers an objective method to assess the animal’s response to HS and the influence of different climate elements.

A number of equations have been developed to calculate THI, using dry bulb temperature (db°C) and relative humidity (RH, %). For example in sheep, $\text{THI} = \text{db°C} - \{(0.31 - 0.31 \times \text{RH}) \times (\text{db°C} - 14.4)\}$ (Marai et al. 2007). Using this equation, a THI lower than 22.2 is classified as thermoneutral, a THI from 22.2 to 23.3 is moderate HS, and a THI of 23.3 to 25.6 it is referred to severe HS , and extreme severe HS occurs when THI exceeds 25.6 (St Pierre 2003; Marai et al. 2007). Recently, another index, the heat load index (HLI), has been developed. This HLI is more sensitive especially for animals living outdoors as it incorporates the effects of wind movement and solar radiation. The HLI is calculated based on THI and combine with heat radiation heat and wind velocity, such as: $\text{HLI} = 8.62 + (0.38 \times \text{RH}) + (1.55 \times \text{BG}) - (0.5 \times \text{WS}) + e^{(2.4 - \text{WS})}$ when black globe temperature above 25 °C (BG= black globe temperature,◦ C; WS = wind speed, m/s; e = base of the natural logarithm) (Gaughan et al., 2008). As a new index, HLI has been used for sheep (Mengistu et al., 2017), beef (Gaughan et al., 2010) and dairy cattle (Lee et al., 2018) research.

Whenever livestock are exposed to environmental temperatures outside their TNZ, thermoregulatory mechanisms, such as increased respiration rate (RR), are activated to achieve homeothermy. However, if the ambient temperature and humidity continue to increase, body temperature regulation becomes difficult, and core body temperature starts to increase, eventually resulting in HS (Chauhan et al. 2014). Under HS conditions, the animal is forced to make drastic changes in its physiological and behavioral responses such as increased RR and reduced feed intake, to cope with the building heat load and increased core temperature (Aggarwal and Upadhyay 2013). Therefore, core body temperature and RR are often measured along with THI to assess an animal's HS responses. Rectal temperature (RT) and RR are the most sensitive physiological responses that are elevated in response to HS. Even a 1°C increase in RT is enough to impact most animal's growth performance and health parameters (McDowell et al. 1996; Berman 2011; Chauhan et al. 2015). For example, acute HS for 3 hrs can increase broiler chickens' core temperature from 42.0°C, to 42.9°C (Lin et al. 2006). In sheep, chronic HS (28 to 40°C, 30 to 40% RH; 1week) increased lamb RR, RT, skin temperature and decreased feed intake as compared to lambs in the thermoneutral group (18 to 21°C, 40 to 50% RH) (Chauhan et al. 2015, 2016).

2.2 HEAT STRESS AND MEAT QUALITY

In the review by Gregory (2010), he postulated that HS will potentially affect broiler meat quality via the influence of HS on postmortem muscle pH decline rate and ultimate pH (pHu). Post-mortem muscle pH decline is affected by glycogen levels and the rate of glycolysis, which in turn can be affected by preslaughter stress and muscle temperature, respectively (Chauhan and England 2018). However, the impacts of HS on meat quality among different species or breeds of animal are not consistent, possibly because of the variation in thermotolerance. In general, the acceptable temperature range for an animal depends on genetics and environment such as feeding level, housing, air speed and stocking rate (Randall 1993). Recent studies have reported variable meat quality performance during summer in different species and breeds of animals. Meat from ruminants, such as mutton and beef, had lower lightness and higher ultimate muscle pH values, similar to dark firm and dry meat (DFD) during summer (Kim et al. 2003; Mach et al. 2008; Weglarz 2010), while poultry and pig meat had greater lightness, and lower pHu similar to PSE meat during summer (Langer et al. 2010; McCurdy et al. 1996; Gregory 2010).

Most controlled HS experiments have focused on poultry (broiler or turkey) meat quality, and the results of HS impacts on meat quality parameters are variable even within these species. As summarized in Figure 1, out of the 23 publications reviewed, 9 publications reported a negative effect of HS on the meat quality and 3 studies reported no significant effect (Figure 1). Interestingly, recent research (section 3.2) has reported some new phenomenon and mechanisms for meat quality changes under HS conditions which may be responsible for the variable effects on carcass quality characteristics and meat quality attributes.

2.2.1 HEAT STRESS AND CARCASS CHARACTERISTICS

As a result of adaptive responses to chronic HS, animals generally reduce feed intake in an attempt to decrease metabolic heat production (Marai et al. 2007), which has implications for carcass fat deposition, carcass yield and intramuscular fat content

(IMF). These impacts on carcass characteristics have been reported both in monogastrics and ruminants, and HS has been well known to reduce feed intake and carcass yield in poultry (Lu et al. 2007; Quinteiro-Filho et al. 2010; Zhang et al. 2012; Imik et al. 2012), pigs (Colditz and Kellaway 1972; Spencer et al. 2003; Pearce et al. 2013), goats (Sivakumar et al. 2010; Lu 1989); cattle (O'Brien et al. 2010; Maloiy et al. 2008) and sheep (Maloiy et al. 2008). The magnitude of changes in carcass characteristics may vary between different species, while overall, HS-induced carcass yield loss has been estimated to cause extensive economic losses to livestock industries (St Pierre 2003). Long term HS also results in decreased subcutaneous fat and lower IMF levels, which may assist the animal with better heat dissipation rates (Ma et al. 2015). For example Lu et al. (2007) demonstrated that Arbor Acres (AA) broilers' breast IMF decreased when birds were exposed to 34°C HS conditions for 3 weeks. Combining with the reduction of fat content, lower acetyl coenzyme A carboxylase enzyme and L (+) P-hydroxyacyl CoA dehydrogenase activity were also reported in a pig HS experiment (Ma et al. 2015). Pearce et al. (2011) reported lower lipolytic enzymes activity in a pig HS experiment, which was independent of the HS-induced reduction in feed intake. Conversely, no significant impact of HS on broiler leg intramuscular fat was reported when birds were exposed to 32°C or 22°C for 3 weeks with ad libitum feeding (Baziz et al. 1996). Similarly, in goats there was no significant effect of one month of out-shed feeding (exposed to THI 73.5-86.5) on IMF contents compared with in-shed feeding (exposed to THI 69.9-74.9) (Archana et al., 2018). The absence of any effects on goats could be because of the better ability of both goat breeds to cope with HS as both breeds were indigenous Indian breeds that have better thermotolerance. Mader et al. (1999) and Ponnampalam et al. (2016) also did not observe any difference in subcutaneous fat thickness over the longissimus lumborum in cattle, and carcass fat score for lambs, respectively, between HS (28 to 40°C, 30 to 40 RH, 1 week) and TN groups. Interestingly, the carcass weight is significantly impacted by HS due to the reduction in feed intake, but the impacts on carcass composition are equivocal and need further research under controlled conditions. However, some the variation in carcass characteristic under HS conditions may be attributed to the inherent differences in heat dissipation capacity of different species/breeds and the severity and length of the HS conditions imposed. Lu et al. (2007) demonstrated that IMF of a better heat adapted chicken breed (Beijing You) was less impacted by HS compared with a high production breed (Arbor Acres). Similarly, in ruminants, Archana et al. (2018) suggested that higher adaptability of indigenous goat breeds to HS could explain why HS had no impact on majority of carcass characteristics.

2.2.2 HEAT STRESS AND POSTMORTEM MUSCLE METABOLISM

After an animal is harvested for meat, two major changes occur to skeletal muscle; physical structural changes, and biochemical changes due to cessation of blood flow and oxygen supply, and lack of glucose supply. However, despite these constraints, skeletal muscle endeavors to achieve premortem homeostatic balance and continues to synthesize and utilize ATP through the metabolism of stored glycogen (England et al. 2013), which is the main source of energy used to generate glycolytic substrates in postmortem muscle. This futile effort of muscle to maintain homeostatic control culminates in accumulation of lactate and hydrogen ions, as pyruvate can no longer enter the mitochondria, as the electron chain has stopped working due to a lack of oxygen (England et al. 2013; Cheah and Cheah 1971). Consequently, there is a decline in muscle pH as lactate and hydrogen ions accumulate (Tarrant 1981). The regulation of these biochemical processes is critical in determining the quality of meat. Any deviation from the normal rate and extent of postmortem metabolism or glycolysis may lead to poor meat quality development, such as faster pH decline and lower pHu which results in PSE meat (Briskey et al. 1964); and meat with a high pHu called DFD, and dark-cutting in ruminants (Tarrant 1989), both of which are inferior in quality and more prone to bacterial spoilage.

In terms of metabolic perturbations, HS leads to elevated plasma glucocorticoid (cortisol) concentrations due to an activation of the hypothalamic–pituitary–adrenal axis. The secretion of cortisol stimulates physiological adjustments that enable an animal to tolerate the stress caused by the hot environment (Christison and Johnson 1972). Generally, animal blood cortisol concentrations will rise as the ambient temperature and exposure time increases (Kadim et al. 2014; Quinteiro-Filho et al. 2010). However, these metabolic changes reported in livestock have not been consistently observed in poultry (Lin et al. 2006). Based on the variation in the metabolic rate antemortem, postmortem muscle physiological and biochemical parameters may vary in heat stressed animals as compared to animals reared under thermoneutral conditions. Heat stress has been implicated in higher muscle glycolysis rate postmortem in broilers transported during summer (Xing et al. 2016), and in broilers exposed to chronic heat stress conditions (Aksit et al. 2006). For example, 0.5 hr summer transportation (32-42°C) increased the AMP/ATP ratio of AA broiler breast, leading to increased AMPK (AMP-activated protein kinase) activity and ultimately resulting in a lower pHu value (Xing et al. 2015). Similarly, Liang et al. (2018) reported that broilers under short term high ambient temperature condition (36°C; 1 hr) had higher AMPK activity than thermoneutral group (25 ± 1°C) at 1 hr. postmortem. There are number of HS studies in poultry and pigs that have reported lower pHu or rapid pH decline in postmortem muscle (Zhang et al. 2012; Tang et al. 2013; Wang et al. 2016;

Downing et al. 2017) However, it is intriguing that other studies did not observe any significant effect of HS on muscle pHu (Lu et al. 2007; Owens et al. 2000; Costa et al. 2006; Shi et al. 2017).

Contrary to responses in pig and poultry, the meat of ruminants generally has higher pHu values under both chronic and acute HS conditions. For example, chronic HS caused by seasonal high temperatures was reported to increase the pHu of *psoas major* and *psoas minor* muscles in goats (Omani and Somali) and sheep (Somali and Merino) (Kadim et al. 2008). As discussed previously, these effects of HS could be explained by glycogen depletion before slaughter and higher glycolytic enzyme activity postmortem, since normal pHu (<5.8) muscle has lower glycogen phosphorylase enzyme activity and glycolytic potential at 0.5 hr postmortem compared to muscle with a high pHu ($\geq$ 5.8) (Apaoblaza et al. 2015). Antemortem glycogen content and glycolytic enzyme activity postmortem would explain the difference between pig, poultry and ruminant meat under HS conditions. For example, ruminant longissimus muscle glycogen concentration of 44.5mmol/kg is required to achieve normal pH decline to <5.8 (Apaoblaza et al. 2015), however, HS would result in the depletion of muscle glycogen (Jentjens et al., 2002) leading to high ultimate pH. On the other hand, in chickens, Wang et al. (2016) reported that short term HS (40°C, 1h) had no impact on chicken breast initial glycogen content and HS increased the glycolytic enzyme activity leading to faster rate and greater extent of pH decline.

It is worth noticing that longer heat exposure or higher ambient temperature may not necessarily cause more negative impact on muscle pH and meat quality (section 2.2.3). For example, Xing et al. (2015) observed that the negative impact on broilers' breast gradually weakened as summer transportation time extend from 1 to 4 hrs (Figure 2). Similarly, Tang et al. (2013) demonstrated that 10 hrs heat exposure (40°C) had no impact on broilers' breast pHu, which was contrary to shorter heat exposure time (1 to 5 hrs ; Figure 3). It appears that exposure to extreme HS conditions for a short duration leads to acute stress response accelerating the rate of postmortem muscle glycolysis and greater decline in muscle pHu. However, prolonged exposure to such conditions may lead to adaptation of animals to HS and therefore no adverse effects are observed on postmortem muscle pH decline. Nevertheless, long-term exposure to HS is well known to have implications for animal welfare and may influence consumers decision to buy meat, though it may not necessarily have impacts on meat quality.

2.2.3 HEAT STRESS AND MEAT COLOUR, WATER HOLDING CAPACITY AND WBSF

Heat stress may result in higher pHu, which leads to less shrinkage of the myofilament lattice and results in a darker meat colour (higher light absorption, less light scattering, higher oxygen consumption) (Gregory 2010; Hughes et al. 2019). Though there are limited studies with controlled temperature conditions focusing on the effect of HS on ruminant meat quality, some studies have demonstrated that HS has negative effect on meat colour, water holding capacity and results in higher pHu value. For example, studies by Kadim et al. (2004, 2007, 2008, 2014) reported that acute and chronic HS decreased goat and sheep meat lightness, with lower WHC and increased toughness. Similarly, Liu et al. (2015) also reported that grazing sheep without access to shade produced meat with a higher pHu and poor overall quality (as summarized in table 1). Although the negative effects of HS on ruminant meat can be similar to those responses observed in DFD meat, which has higher WHC compared to normal meat, the responses noted in heat stressed (seasonal comparisons and summer transportation) ruminant meat had lower WHC (Kadim et al. 2008, 2014), which is usually associated with PSE-like meat. On the other hand, HS increases the rate of pH decline in postmortem muscle in broilers and pigs, which results in higher lightness and lower WHC. For example, acute HS (32°C, 2h) significantly accelerated the pH_{15min} decline in broiler breast muscle and degraded meat quality attributes such as higher drip loss (72h postmortem), higher breast meat colour and lower sensory score (Sandercock et al. 2001). Similar trends were also was observed in chronically heat stressed broiler and turkey meat that was paler in colour and had a lower WHC under seasonal HS conditions (Lu et al. 2007). In pigs, chronic HS (35°C, 78% RH; 30 days) increased LTL WBSF and decreased intramuscular fat content (Shi et al. 2017; Table 2).

Interestingly, although the majority of publications have reported negative impacts of HS on meat quality, recent studies suggest that the negative impacts of HS (both under acute and chronic conditions) on meat quality are not consistent and are even contradictory. Some of these variable effects can be attributed to differences in ambient temperature, relative humidity, and exposure time to high environmental temperature between individual studies. Ponnampalam et al. (2016) reported that 7 days of cyclic HS (28-40 °C, 30-40% RH) did not negatively influence lamb muscle pHu and TBARS levels. Northcutt et al. (1994) observed that broilers reared at an ambient temperature of 40°C had better WHC of *pectoralis major muscle* compared to control (25 °C). Moreover, it appears that meat quality is also affected by the duration of exposure to heat stress conditions which may result in variable meat quality parameters. For example, Tang et al. (2013) measured the meat quality of the *pectoralis major* of broilers under different heat (37±1°C) exposure time before slaughter and found that the muscle lightness, cooking loss, and WBSF values were maximum after 3-5 hrs of heat exposure. After 10 hrs. of heat exposure, muscle quality parameters showed a trend towards recovery and better meat quality was observed (Figure 3). Similar trends were also reported by Xing et al (2015), where 0.5 hrs of transportation during summer resulted in lower chicken meat quality parameters, and the birds transported for 4 hrs showed similar breast lightness, WHC and pHu relative to the non-transportation group. Zhang et al. (2019) also demonstrated that broilers' breast meat quality was affected mostly at 36 °C heat exposure. As the ambient temperature increased from 38 °C to 40 °C, certain meat quality parameters showed a reverse trend and improved in quality, and the plasma cortisol level had no increase between 38 °C and 40 °C (Figure 4). Therefore, acute HS is more likely to affect broilers' meat quality as extreme high temperatures or acute heat exposure does not allow the adaptive responses to HS to occur, whereas chronic HS may provide opportunities for animals to adapt thus having less impact on meat quality (Sandercock et al. 2001). However, this does not undermine the implications of heat stress on animal welfare irrespective of impacts on meat quality.

2.2.4 HEAT STRESS AND MEAT SAFETY

There are a limited number of studies that have investigated the effect of HS on meat safety, but it is generally accepted that high ambient temperature and humidity present favorable conditions for pathogen colonization which may lead to safety risks for meat and by-products. Chronic stress may influence the course of animal infection and/or the susceptibility to a microorganism (Elenkov and Chrousos 1999); alter the hosts intestinal barrier susceptibility to pathogenic bacteria; and increase intestinal permeability and luminal attachment for bacteria (Bailey et al. 2004). Higher catecholamine and glucocorticoid (stress hormone) secretion may affect the animals intestinal barrier function and microbial environment (Verbrugghe et al. 2012). Secretion of norepinephrine also accelerates intestinal motility, colonic transit and transepithelial ion transport, which may also influence gut microbial populations

(Mizuta et al. 2006). Apart from the direct effects of stress, higher pHu caused by HS offers a conducive environment for microbial growth. Faucitano et al. (2010) found that DFD meat had highest total aerobic mesophilic and presumptive lactic acid bacteria counts when stored for 35 days at 4 °C following vacuum packaging. Similar results have also been reported in broiler meat (Allen et al. 1997).

3. MANAGEMENT STRATEGIES FOR ALLEVIATION OF HEAT STRESS ANTEMORTEM

In general, HS is the result of an imbalance between heat production and heat loss mechanisms. Therefore, in addition to physical modifications of the animal's environment to minimize the exposure to heat, various mitigation strategies need to be targeted to either reduce heat production in the body or to enhance heat loss from the body, to achieve homeothermy. The strategies to reduce HS have been broadly classified as environmental modifications, genetic selection for improving thermotolerance, and nutritional strategies to improve feed intake and decrease metabolic heat production (Beede and Collier 1986; Chauhan et al. 2015).

3.1 SHADE AND SHELTER MANAGEMENT

Provision of shade is likely the most direct way to protect animals from direct and indirect exposure to solar radiation while not necessarily reducing the air temperature. For example, man-made shelters can significantly reduce the risk of HS in cattle compared with lack of shade availability (Van laer et al. 2014; Eigenberg et al. 2005). The provision of shade not only ameliorates the heat load of cattle (Gaughan et al. 2010; Mader et al. 1999) but also reduces the mortality in extreme weather conditions (Darrell Busby 1997). A limited number of studies have investigated the effects of shade on meat quality, and it has been observed that provision of shade produced sheep meat with less high pHu and better WHC (Liu et al. 2012). However, there were no differences in growth performance, carcass fat percentage (Mader et al., 1999), or meat quality of shade feedlot cattle as compared with conditions of no shade (DiGiacomo et al., 2014). While shade can be effective in amelioration of some of the negative impacts of HS under hot and dry conditions, but it may not be as effective under hot and humid conditions (Renaudeau et al. 2012; Gaughan et al. 2010). In general, provision of shade or shelter is recommended in the areas where ambient temperature exceeds 24°C, to promote the welfare of farm animals and prevent production losses due to HS (Silanikove 2000). While provision of shade can be an effective method to reduce heat load in dairy cows even in temperate climate zones such as under New Zealand summer conditions (Fisher et al. 2008; Kendall et al. 2006; Schütz et al. 2008), the beneficial effects of shade for meat quality during summer in temperate zones requires further research.

3.2 EVAPORATIVE COOLING AND CONVECTION

Evaporative and convective cooling are effective means of heat loss from the animals body and can be utilized to cool animals both on farm and during lairage at the processing plant. It involves the provision of air movement and water-cooling systems. Recent research in broilers and turkeys has shown that better growth performance can be obtained with provision of optimal ventilation in general (Yahav et al. 2005; Renaudeau et al. 2012). Combining a well-oriented, semi-open building, with a high and well isolated roof will provide natural ventilation to the animals. Among other strategies, fan systems with shower like sprinkler-misters can be used to reduce the ambient temperature in low RH areas, thus reducing the heat load on animals. The sprinkler-fan system could improve feed intake of dairy cows by 7% to 10% as a result of lower body temperature and respiration rates (Aggarwal and Upadhyay 2013). During summer, water cooling could be an effective strategy to alleviate the negative effects of HS on meat quality. Long and Tarrant (1990) found showering of pigs with water brought about a 2°C temperature drop in pig LTL muscle after slaughter in summer, which was sufficient to reduce paleness and drip loss in loin chops. Xing et al. (2016) pointed out that 10 min of water spray after transportation on a hot day produced a significant reduction in broiler HS and improved chicken meat quality. However, these responses to water cooling are less pronounced or absent in humid regions (Renaudeau et al. 2012).

3.3 NUTRITIONAL STRATEGIES

One of the largest negative effects of HS on animal production is the reduction in feed intake, therefore dietary interventions targeting improved energy metabolism may alleviate some of the negative effects of HS on animal growth and meat quality characteristics. Similarly, HS is known to cause oxidative stress in poultry (Mujahid et al. 2009), pigs (Liu et al. 2018), sheep (Chauhan et al. 2015), and cattle (Bernabucci et al. 2002; Bernabucci et al. 2010; Garner et al. 2017). Therefore, supplementation with dietary antioxidants provides an opportunity to alleviate some of the negative impacts of HS. Antioxidants play an important role in preventing oxidative damage at the cellular level. Cellular defense against oxidative damage exists at four different levels: scavenging free radicals, chelation of metal ions, regeneration of antioxidants, and repair of oxidized molecules (Chauhan et al., 2014). Antioxidants, such as phenolic compounds and alkaloids from plant extracts, react with radicals to form more stable compounds via hydrogen proton or directly donate electrons to react with radicals, which could inhibit or delay oxidative chain reactions (Prakash et al. 2013). Some antioxidants not only play a role in scavenging free radicals directly, but also play an important role in enzyme antioxidant systems. For example, quercetin inhibits inducible nitric oxide synthase (iNOS) activity and improves antioxidant enzyme activity which may improve raw meat colour stability and flavor via oxidation inhibition (Goliomytis et al. 2014).

Additionally, dietary manipulation to alter systemic insulin sensitivity may be an effective strategy to reduce the HS impacts, as appropriate insulin action is one of the key components of successfully adapting to and surviving a heat load (Rhoads et al. 2013). Recent research has demonstrated that the negative impacts of HS are not only associated with reduction of feed intake, but that there are direct impacts of HS on energy metabolism, with a shift towards increased carbohydrate use and reduced lipid oxidation (see review by Rhoads et al. (2013)). Therefore, diets or nutritional supplements promoting glucose use may be beneficial to reduce the negative impacts of HS. Other additives to the diet could either improve body water balance or improve body condition preslaughter, each of which may improve meat quality attributes. Some of the potential nutritional supplements known to improve meat quality are briefly reviewed in this part.

3.3.1 ELECTROLYTES

As discussed previously, when body temperature increases during HS conditions, evaporative heat loss plays the main role of heat dissipation, which often results in respiratory alkalosis due to hyperventilation, and dehydration due to excessive salivation (West 2003). This ultimately leads to increased blood pH as carbon dioxide partial pressure and total concentration decreases. This adverse respiratory alkalosis and dehydration situation could be relieved by electrolyte supplementation (Teeter et al. 1985; Sawka and Montain 2000). Aqueous electrolyte solution has been shown to improve broiler growth performance under stressful conditions and also subsequent meat quality (Whiting et al. 1991; Deyhim and Teeter 1991; Belay and Teeter 1993; Ait-Boulahsen et al. 1995). Kumar et al. (2010) showed that the supplementation of ascorbate in the diet in addition to electrolytes alleviated oxidative stress in buffaloes and helped to boost the cell mediated immunity under HS conditions. In cattle, electrolyte supplementation alleviated carcass yield loss during transportation stress and reduced DFD meat frequency (Schaefer et al. 1990, 1997). However, it should be noted that antemortem electrolyte therapy in cattle had no significant effect on the beef flavor, juiciness, WBSF and overall palatability rating of beef (Jeremiah et al. 1992).

3.3.2 VITAMIN E

Vitamin E (Vit E) is the most important lipid soluble chain breaking antioxidant present in cell membranes and prevents the oxidative damage to lipids and proteins by directly scavenging free radicals and reducing lipid peroxide formation. Pervious research has demonstrated that Vit E supplementation leads to a significant reduction in meat product oxidation and improvement in colour stability (Mitsumoto et al. 1991; Guerra-Rivas et al. 2016). Several studies have shown that Vit E supplementation with or without selenium (Se), may improve physiological responses and animal performance under HS conditions. For example, Sivakumar et al. (2010) found that Vit E and Vitamin C supplementation improved goat RR, feed intake and cortisol levels under HS conditions (40C, 30% RH; 21days). In a series of experiments in sheep and pigs, our lab has demonstrated that the combination of supranutritional Vit E and Se supplementation can be used to reduce the negative impacts of HS (Chauhan et al. 2015;

Liu et al. 2016). High levels of Vit E and Se supplementation significantly alleviated HS effects in sheep via improving feed intake and antioxidant enzyme activity (Chauhan et al. 2015). Similarly, in another study in pigs, Liu et al. (2016) demonstrated that high levels of dietary Se and Vit E can reduce both oxidative stress and intestinal leakiness. However, the effect of Vit E and Se supplementation on meat quality performance under HS conditions requires further research as the limited research so far has indicated equivocal results. Ponnampalam et al. (2016) did not observe any significant effect of Vit E and Se supplementation on the meat quality of lambs finished under hot summer conditions; but recent research by the same group reported that supranutritional Vit E supplementation during finishing under HS conditions improved aged lamb meat colour stability and reduced the brownness formation (Baldi et al. 2019). Furthermore, lambs supplemented with supranutritional Vit E during the finishing phase had higher muscle Vit E content as compared to lambs finished on Lucerne diet, however, there was no difference in lipid oxidation between the two groups.

3.3.3 FLAVONOIDS

Flavonoids exist widely in plant tissues and have the most variety compared to other polyphenol compounds. According to their basic structure, flavonoids generally can be classified into flavones, flavanones, anthocyanidins and flavanols (Lotito and Frei 2006). Among the various flavonoids, catechins have been the most commonly used in recent research on animal diets (Perumalla and Hettiarachchy 2011). In addition to their chain breaking antioxidant function, catechins are also involved in the regeneration of endogenous antioxidants like Vitamin E. For example, dietary supplementation of 2mg/kg green tea (catechins) for 4 weeks in rats, increased the plasma and tissue alpha-tocopherol concentration (Frank et al. 2006). In vitro, catechins spared alpha-tocopherol both by inhibiting its free radical mediated oxidation and by regenerating it from its a-tocopheroxyl radical (Frank et al. 2006). In human research, Vitamin E-sparing and regenerating effects were observed for green tea extracts (Zhu et al. 1999). In animal diets, supplementation with catechins has been shown to enhance meat antioxidant capacity and improve meat quality. For example, catechins supplementation (3000–4000 mg tea catechin (tea catechin/kg fed for 40-60 days) improved goat meat (fresh) colour, oxidation stability and WHC (Zhong et al. 2009). Tang et al. (2001) further found that 200 and 300 mg/kg tea catechin supplementation was effective in significantly delaying lipid oxidation as compared to the control in chicken heart, liver, thigh meat and breast, and 300mg/kg TC had antioxidant capacity equal to 200 mg/kg of Vitamin E diets. However, 10-100 mg/kg feeding of green tea polyphenols had no significant effects on pork quality, plasma antioxidant capacity and tissue Vitamin E level (Augustin et al. 2008).

In HS studies, dietary genistein (one of the isoflavones) supplementation (400 and 800 mg/kg) was reported to reduce the negative effects of cyclic heat (34°C) stress on Japanese quail carcass yield and serum TBARS level (Onderci et al. 2004). Another study by Kamboh et al. (2013; 2014) reported that 5 mg/kg genistein feeding, and 10 or 20 mg/kg genistein-hesperidin feeding in broiler groups lowered breast HSP70 mRNA expression under summer stress and had higher WHC (%), but 20 mg/kg genistein-hesperidin diets increased broiler breast meat lightness values. Further research is required to demonstrate the potential benefits of flavonoids supplementation in ruminant diets to improve meat quality during summer.

3.3.4 BETAINE

Betaine is a quaternary ammonium compound and present in vertebrates' viscera and amniotic fluid. It can be extracted from sugar beets or synthesized by chemical reactions. Betaine was adapted as a replacement for methionine and choline to play a role of methyl donor and osmoprotectant in poultry and fish diets as early as the 1970s (Fernandez-Figares et al. 2002; Kidd et al. 1997). Dietary betaine supplementation has been shown to increase carcass leanness (muscle accretion) and decrease carcass fat thickness in pigs and poultry, as reviewed by Eklund et al. (2005). However, recent studies showed that betaine supplementation for 2 days pre-transport did not improve broiler meat quality and growth performance (Wray Cahen et al. 2004; Huang et al. 2006; Downing et al. 2017; Park and Park 2017).

During summer, dietary betaine enhanced rabbits growth performance during high ambient temperatures and decreased RT and RR (Hassan et al. 2011). Betaine had HS ameliorative effect in a dose dependent manner such that a lower dose of betaine successfully ameliorated the increased skin and core temperatures, heart rates and RR, however, higher betaine doses had negative impacts on theses parameters (DiGiacomo et al. 2014, 2016). Research by He et al. (2015) found that supplemental dietary betaine reduced the effect of chronic HS on broilers body weight and fat deposition. In our lab, Liu et al. (2016) found that the combination of Se, Vitamin E, Cr and betaine (based on standard diets) could reduce the loss of body reserve of lactating sows during summer. And Shakeri et al. (2019) demonstrated that 1g/kg betaine significantly improved the growth performance of Ross-308 chicken and under cyclic heat stress condition (33 °C, 45-60% RH; 35 days). Dietary betaine also could reduce cadmium-induced oxidative stress (rats and broilers) via increasing CAT, GPx and SOD activity (Alirezaei et al. 2011, 2012a, 2012b). On the contrary, some studies reported that betaine supplementation did not change pig lipid metabolism (Fernandez-Figares et al. 2002;

Wray Cahen et al. 2004). As dietary betaine may contribute to an animal's antioxidant capacity, it therefore could affect animal meat quality characteristics such as colour, WHC and lipid oxidation. The study by Liu et al. (2015) suggested that betaine and guanidinoacetic acid supplementation could increase the pork pH_{24h} and improve meat WHC and WBSF values. In broilers, dietary betaine improved meat pH_{24h} and WHC (Fu et al. 2016). However, further studies are required to demonstrate similar effects of betaine on meat quality of ruminants finished during summer.

3.3.5 OTHER POTENTIAL FEED ADDITIVES FOR THE PREVENTION OF HEAT STRESS DAMAGE

In addition to the existing feed additives, other antioxidant compounds or growth promotion additives might also play an important role in prevention of HS and improvements in meat quality. These additives have been shown to improve antioxidant capacity in animal feeding experiments but require further experimentation in animals finished under HS conditions. For example, adiiton of 50-200 mg/kg lycopene (red carotenoid) to diets significantly decreased broiler muscle TBARS, CAT, GSH-Px levels and growth performance (Marzoni et al. 2014; Jiang et al. 2015). Other studies involving meat sensory tests showed that supplementation with 15mg/kg β-carotene significantly increased cooked chicken meat juiciness as compared with 200 mg/kg Vitamin E supplementation, and WBSF as compared with control group, however, on the other hand, β-carotene diets had negative effect on cooked meat odor and flavor (Ruiz et al. 2001). Carnosine, a dipeptide natural antioxidant, significantly improved pig plasma GSH-Px, SOD activity and muscle glycogen content when supplemented in the diet at 100 mg/kg (Ma et al. 2010). Looking at the improvements in animal antioxidant capacity following supplementation of these additives, it is tempting to hypothesize that these feed additives may have potential benefits on meat quality of animals finished during HS conditions and therefore warrant further investigation.

4. CONCLUSION

HS is one of the greatest challenges facing livestock production and is likely to be exacerbated by rising ambient temperatures due to climate change. There has been vast interest from an animal production and welfare point of view in the development of HS mitigation strategies to reduce the economic losses incurred by the global livestock industry during summer. Significant progress has been achieved in understanding the impacts of HS on physiological and metabolic status of animals affecting animal performance. Research in recent years has been focused on HS impacts on animal product quality and suitable interventions to mitigate these negative impacts. There is some evidence that HS preslaughter may lead to higher incidence of PSE in pigs and poultry, and DFD in ruminants. However, these influences are not consistent across different studies and vary depending on the severity and duration of HS exposure. There is a dearth of well-designed controlled environmental studies comparing impacts of high ambient temperature on meat quality of ruminants. These research gaps need to be addressed and would be a step forward before developing suitable strategies to alleviate HS impacts on meat quality. Nevertheless, there are some nutritional strategies that have been found effective to ameliorate some of the negative effects of HS on animal physiology and metabolic responses, such as electrolytes, flavonoids, Vitamin E and betaine.

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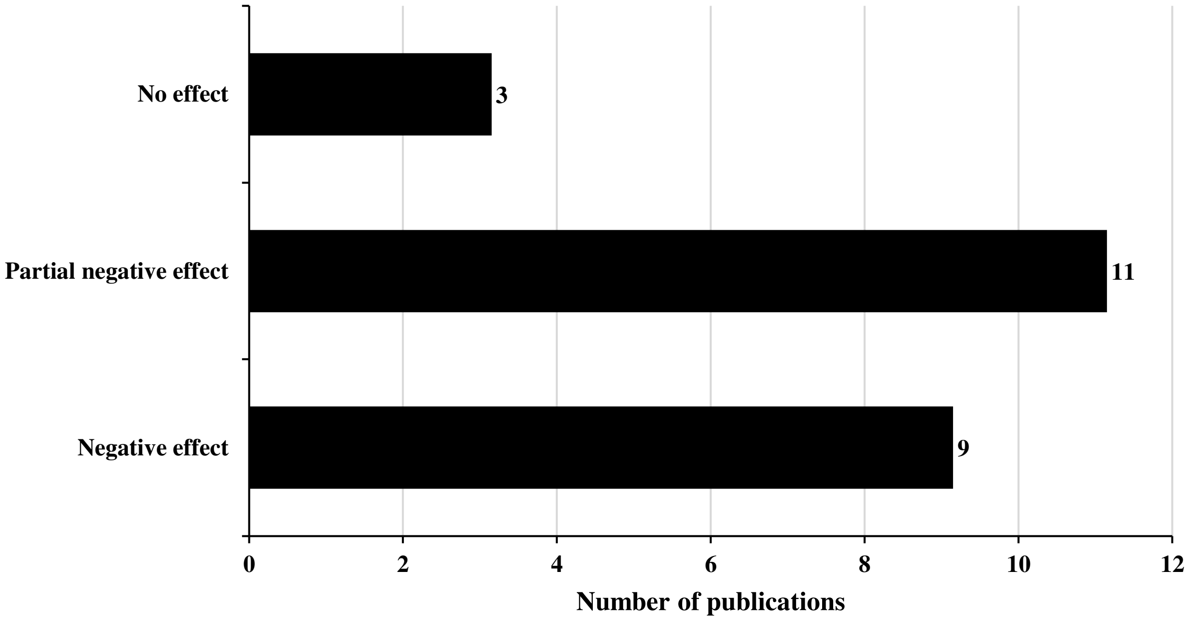

Figure 1. Summary of effects of heat stress HS in animals on subsequent meat quality across 23 studies.

Negative effect= (Sams and McKee 1997, Kadim et al. 2004, Akşit 2006, Kadim 2007, Feng et al. 2008, Kadim et al. 2008, Dai et al. 2009, Zhang et al. 2012, Kadim et al. 2014);

Partial negative effect= (Holm and Fletcher 1997, Sandercock 2001, Debut et al. 2003, Marıa et al. 2006, Lu et al. 2007, Saha et al. 2013, Shi et al. 2017, Imik et al. 2012, Tang et al. 2013, Xing et al. 2015, Zhang et al. 2019);

No effect= (Froning et al. 1978, Owens et al. 2000, Zeferino et al. 2013);

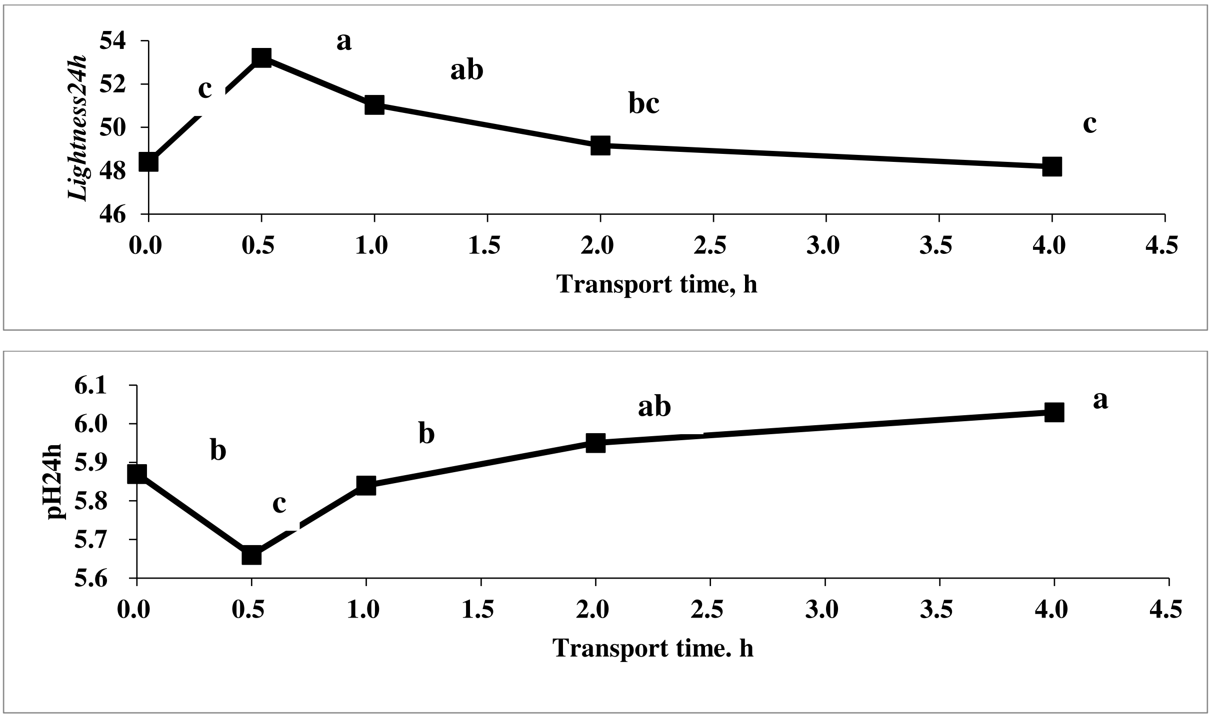

Figure 2. Effect of transport time on *pectoralis major* muscle pH and lightness (L*) at 24 hrs post-slaughter (pH24h, Lightness24h respectively) for AA broiler chickens (market age) exposed to different transportation conditions (40-42°C); n=21, 21, 21, 17, and 14 chickens for control, 0.5h, 1h, 2h, and 4h transport groups, respectively (Adapted from Xing et al., 2016). a-c means the significant difference ($P < 0.05$) within different transport time

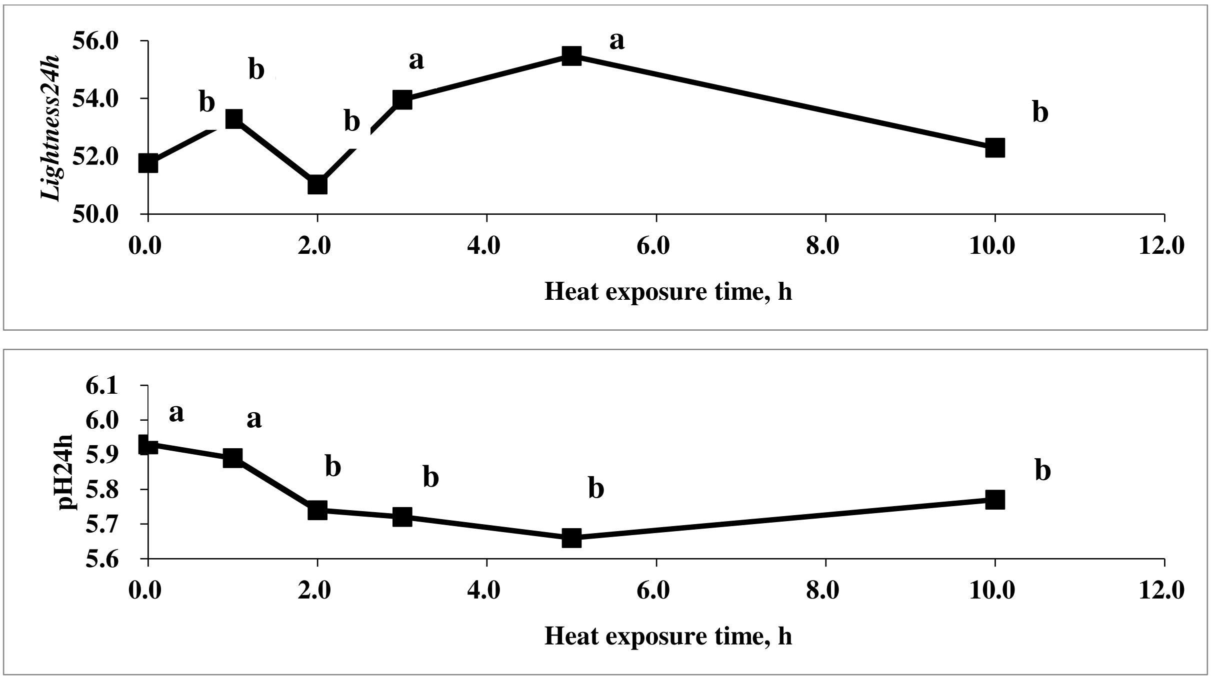

Figure 3. Effect of time of exposure to acute HS (40°C) before slaughter on *pectoralis major* muscle pH and lightness at 24 hrs post-slaughter (pH24h, Lightness24h respectively) for AA broiler (28 days age) (n=10). Adapted from Tang et al.(2013). ab, indicates a significant difference (*P* < 0.05) between heat exposure times.

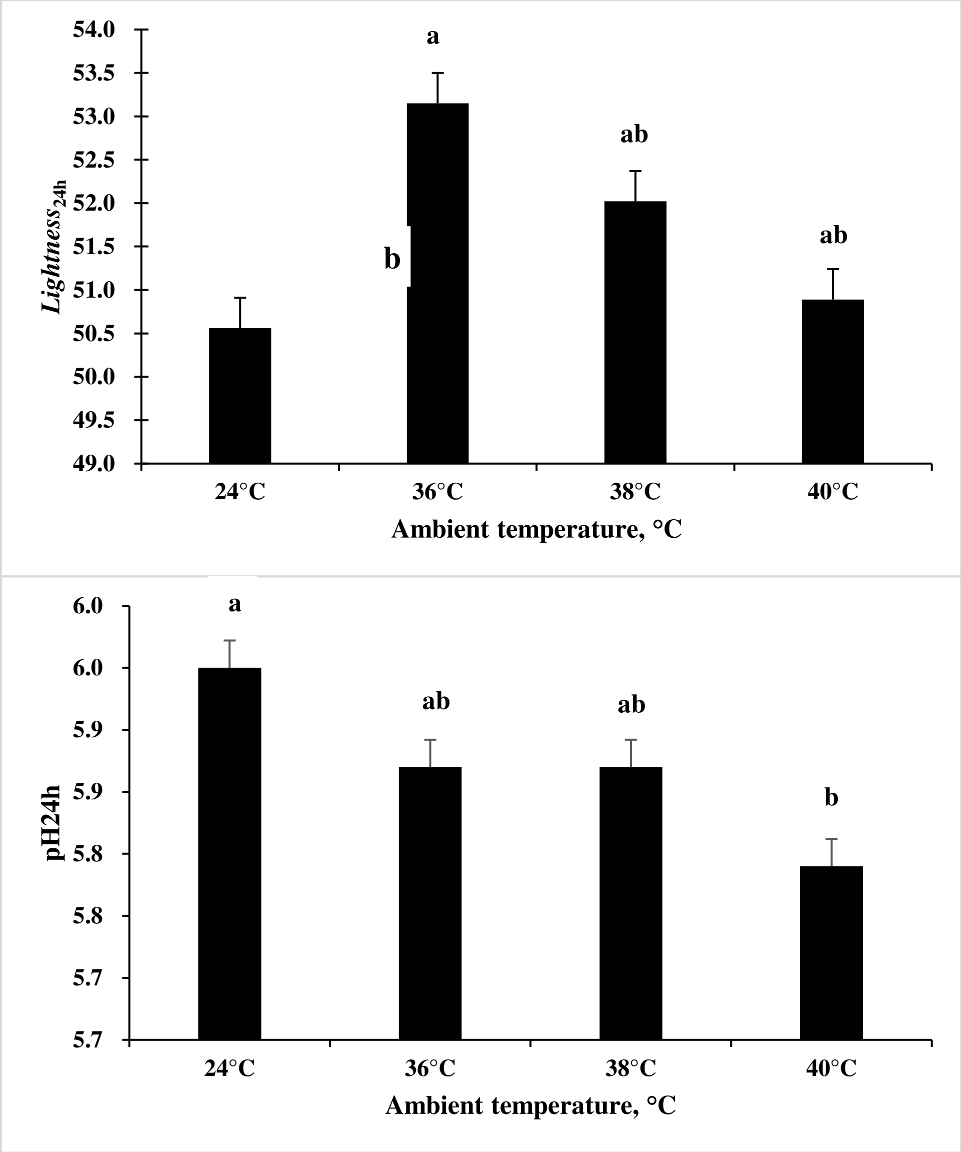

Figure 4. Effect of different temperature of acute heat stress on *pectoralis major* meat lightness and pHu at 24 hrs post-slaughter (pH24h, Lightness24h respectively) for AA broiler (42 days) (n=12) (Zhang et al., 2019). ab, indicates a significant difference (*P* < 0.05) between heat exposure times.

Table 1. The effect of acute and chronic heat stress on ruminant growth performance and meat quality

Authors	Breed	Treatment	Muscle	Observation
Kadim et al. (2008)	Goat: Omani, Somali Sheep: Somali, Merino	Hot season (35°C, 47%RH) Cool season (21°C, 59%RH)	Psoas major and minor	Hot season decreased meat lightness (24 h postmortem), WHC, increased MFI and pHu.
Kadim et al. (2014)	Dhofari goats	Summer transportation (6 hrs. 42°C)	Longissimus thoracis et lumborum	Pre-slaughter transportation during high ambient temperatures increased meat pHu decreased meat lightness, WHC and WBSF at 48 h postmortem.
Ponnampalam et al. (2016)	Poll Dorset x [Border Leicester x Merino] lamb	HS:28-40°C TN:18-21°C 1 week	longissimus lumborum	HS had no significant influence on pHu of meat and slaughter or carcass weight. TBARS also has no significant different.
Archana et al. (2018)	Osmanabadi and Salem Black goat	Out-shade and in-shade feeding 28 to 40 °C and 29 to 58%RH, 1 month	Longissimus thoracis et lumborum	HS significant increased meat pHu (24 h postmortem), WBSF (12 h postmortem) and decreased lightness at 12 h postmortem.

Kadim et al. (2004)	Omani beef	Hot season 34.3±1.67 °C, 48.87.57% RH Cold season 21.2±1.40 °C, 57.91.61% RH	Longissimus thoracis	Ambient temperatures of approximately 35°C elevated meat pHu, darkened meat colour (lightness reduced) and decreased cooking loss than those under 21°C.

HS=heat stress, TN=thermoneutral, RH=relative humidity, WHC=water holding capacity, MFI=myofibril fragmentation index, WBSF= warner–bratzler shear force, TBARS=thiobarbituric acid reactive substances.

Table 2. The effect of acute and chronic heat stress on broiler and pig meat quality

Author	Breed	Stress treatment	Muscle	Observation
Xing et al. (2015)	Arbor Acres broiler	Summer transportation; 0-4 h.	Pectoralis major	0.5h summer transpiration had the most negative effect on broiler meat quality (lightness, cooking loss and drip loss) but not include redness and yellowness. Meat quality parameters got closer to control group as transportation time and death rate increased.
Sandercock et al. (2001)	Broiler (35d, 63d age)	HS:32°C, 75% RH TN:21°C, 75%RH 2 h.	Pectoralis major	HS only increased meat drip loss (age of 35 days) and hemorrhage score, but had no effect on colour score and sensory test results.
Tang et al. (2013)	Arbor Acres broiler	HS:37°C; 0 to 10 h TN:22°C.	Pectoralis major	Acute HS had significant effect on chicken meat quality. Meat had the poorest quality under 2 h acute HS condition. As exposure time of HS extended, the negative effect of HS gradually decreased.

Zhang et al. (2019)	Arbor Acres broiler	HS:36°C, 38°C, 40°C; TN:25°C 1 h., 2 h.	Pectoralis major	36°C HS significant increased chicken meat lightness and cooking loss. In 40°C temperature, chicken meat quality parameters had no significant difference with control group (25°C)
Lu et al. (2007)	Arbor Acres broiler, AA Beijing You chicken, BJY	HS:34°C TN:21°C 3 weeks.	Pectoralis major	The data showed that chronic heat exposure had negative effects on growth performance, breast yield, and meat quality of AA broilers, but it had no significant influence on growth and meat quality in the local, slow-growing chickens.
Aksit et al. (2006)	Broilers	HS: 34°C TN:22°C -28°C 4 weeks.	Pectoralis major	22-28°C and 34°C HS both had negative effect on chicken meat pHu and lightness and growth performance including food consumption and conversion.
Shi et al. (2017)	American Landrace barrows	HS:35°C, 78% RH TN:22 °C, 81%RH 30 days.	Longissimus dorsi	HS significantly decreased feed intake ($P<0.05$), but meat quality had no difference with control group (22°C), except intramuscular fat contend.

HS=heat stress, TN=thermoneutral,