Poultry Science

Heat stress and poultry production: a comprehensive review

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ABSTRACT The impact of global warming on poultry production has gained significant attention over the years. However, our current knowledge and understanding of the mechanisms through which heat stress (**HS**) resulting from global warming affects the welfare, behavior, immune response, production performance, and even transgenerational effects in poultry are still incomplete. Further research is needed to delve deeper into these mechanisms to gain a comprehensive understanding. Numerous studies have investigated various biomarkers of stress in poultry, aiming to identify reliable markers that can accurately assess the physiological status and well-being of birds. However, there is a significant amount of variation and inconsistency in the results reported across different studies. This inconsistency highlights the need for more standardized methods and assays and a clearer understanding of the factors that influence these biomarkers in poultry. This review article specifically focuses on 3 main aspects: 1) the neuroendocrine and behavioral responses of poultry to HS, 2) the biomarkers of HS and 3) the impact of HS on poultry production that have been studied in poultry. By examining the neuroendocrine and behavioral changes exhibited by poultry under HS, we aim to gain insights into the physiological impact of elevated temperatures in poultry.

Key words: biomarker, glucocorticoid, heat stress, maternal effect, poultry, welfare

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INTRODUCTION

The poultry industry contributes significantly to the United States and global economy with consumption rate higher than beef or pork in the United States (2023). Poultry exports are expected to increase by 8 million pounds for turkey and 158 million pounds for broiler while beef and pork export are expected to decrease in the United States (Hahn et al., 2022). Poultry, including chicken, duck, and turkey, is a major source of protein in the form of meat and egg for many people around the world. However, there are various factors that impact the production of poultry meat and eggs. Temperature is one of the most significant stressors impacting poultry production having significant effects on the health and productivity of poultry (Quinteiro-Filho et al., 2012; Hosseini-Vashan et al., 2020; Hu et al., 2022; Sun et al., 2023). Economic loss in agricultural production as a result of high temperature is estimated to be over $1 billion in 2011 (Hatfield et al., 2014). Climate change can also affect animal productivity indirectly by causing the production of feed with lower quality and outright scarcity of feed stuff (reviewed by Vandana et al., 2021). This is expected to negatively impact fertility and growth performance. Selective breeding over the decades resulted in fast growth and high feed efficiency in poultry, but these traits are associated with high metabolic rates and increased susceptibility to heat stress (**HS**) (Deeb and Cahaner, 2002; Gogoi et al., 2021; Nawaz et al., 2023). Therefore, it is important to investigate the effects of HS on poultry production and to develop strategies or management practices to mitigate its negative effects.

The physiological response to HS in poultry involves the activation of the sympathetic adreno-medullary (**SAM**) pathway that results in the release of catecholamines, such as epinephrine and norepinephrine, and then activation of the hypothalamic−pituitary−adrenal (**HPA**) axis that results in the secretion of glucocorticoids (**GC**) (Li et al., 2022; Mirsaiidi Farahani and Hosseinian, 2022; Oluwagbenga et al., 2022). Several studies have reported the detrimental effect of prolonged exposure to GC resulting from HS on production, performance, egg quality and welfare of the exposed animal (Mashaly et al., 2004; Ebeid et al., 2012; Ma et al., 2014; Mehaisen et al., 2019; Qin et al., 2023; Welay et al., 2023). In addition to these detrimental effects, GC or catecholamines can also be deposited into the egg by the mother (Caulfield and Padula, 2020; Oluwagbenga et al., 2022, 2023b; Lyte et al., 2023). The study of the

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effect of these hormones in eggs has gained a lot of attention over the last 2 decades. Several studies have proven the presence of GC in egg by quantifying them using different assays and methods, however there is lack of validation of these assays and methods (Love et al., 2008; Caulfield and Padula, 2020; Miltiadous and Buchanan, 2021). Early exposure to GC in the eggs can lead to long-term effects on brain activity, productivity, behavior, and immunity (Tilgar et al., 2016; Romano et al., 2021). Determination of GC in eggs has been reported as a tool for phenotypic engineering of the offspring to increase fitness and adaptation to the environment, a process referred to as hormone-mediated epigenetics, has been reviewed (von Engelhardt and Groothuis, 2011; Groothuis et al., 2019). Hormone-mediated epigenetics is a potential tool for adjusting phenotype of the offspring to increase fitness and adaptation to the high temperatures resulting from climate change.

Stress and Poultry Production

Stress is a condition in which an animal attempts to restore homeostasis and this is caused by factors or challenges that disrupt the normal functioning of the body. Poultry, like all animals, are regularly exposed to a variety of stressors including social or environmental factors (reviewed by Scanes, 2016). Poultry are more susceptible to HS especially due to their inability to sweat thereby relying on panting as a means of dissipating heat. The physiological responses to stress in poultry involve the activation of the SAM pathway that results in the release of catecholamines such as epinephrine (**EP**) and norepinephrine (**NE**) from the adrenal medulla (Li et al., 2022). After the SAM, the HPA axis is activated which results in the release of GC, such as cortisol and corticosterone from the adrenal cortex (Li et al., 2022; Mirsaiidi Farahani and Hosseinian, 2022; Oluwagbenga et al., 2022). Historically, cortisol and corticosterone were believed to be the major stress hormones in birds; however, over the past 20 years cortisol has been given considerably less attention in birds with corticosterone being the focus of research. Recently, newer studies reported the presence of cortisol during stress in ducks and their physiological importance in evaluating welfare (Oluwagbenga et al., 2022; Tetel et al., 2022a,b; Oluwagbenga et al., 2023b). Both GCs have positive and negative effects on the body, depending on the duration and intensity of the stressor. However, acute stress can have more positive side effects such as increased alertness, vigilance, and improved immune responses, while chronic stress can lead to a range of negative outcomes that include impaired growth, reproduction, and immune function (reviewed by Romero et al., 2015). Overall, stress is an important factor to consider in poultry production and welfare. By understanding the sources of stress and implementing strategies to minimize it, it is possible to improve the well-being of poultry and enhance the sustainability of poultry production systems.

Neuroendocrine Response to Stress

The SAM Pathway The SAM plays a crucial role in the response of poultry to HS, as it handles the release of catecholamines such as NE and EP upon activation by stressor (Quirarte et al., 1998; Li et al., 2022). These hormones engage in the regulation of various physiological functions, including heart rate, blood pressure, and glucose metabolism, and are released in response to stressors such as high environmental temperature, social interactions, and husbandry practices (Cyr et al., 2009; Carravieri et al., 2016; Müller et al., 2017; Kim et al., 2021). The SAM pathway also controls the fight or flight response. Catecholamines affect muscle contraction and relaxation, and bronchodilation responsible for adapting to changes induced by stressors (reviewed by Dennis, 2016). Changes in the levels and ratio of EP and NE in the body have been used as indicators of an animal's well-being and for evaluating heat stress status of the flock (Yan et al., 2013, 2020), although there are limitations such as sensitivity to handling stress and blood sampling.

The HPA Axis

The HPA axis is responsible for modulating adaptive response to HS that mediate changes in reproduction, metabolism, production, and behavior (Quinteiro-Filho et al., 2012; Park et al., 2018; Al-Sagan et al., 2020; Hosseini-Vashan et al., 2020; Li et al., 2020b; Hu et al., 2022; Sun et al., 2023). The HPA axis is important in the regulation of the hormones for maintaining homeostasis of the body (Nagarajan et al., 2017; Li et al., 2022). Increase in HPA activity might not necessarily be in response to a stressor such as increase in cortisol level after eating and after increased physical activity (Brandenberger et al., 1982; Kiive et al., 2004; Hötting et al., 2016). In all animals, including poultry, the main target gland of the HPA axis during stress response is the adrenal gland for the secretion of GC.

Upon activation of the HPA axis in birds, corticotropin-releasing hormone (**CRH**) and arginine vasotocin (**AVT**) are secreted from the nucleus of the hippocampal commissure and paraventricular nucleus of the hypothalamus respectively (Nagarajan et al., 2014, 2017). Arginine vasotocin is a neurohormone secreted in response to stress in birds and it is structurally and functionally similar to arginine vasopressin (**AVP**) found in mammals (Nagarajan et al., 2014). CRH and AVT act on the anterior pituitary and stimulate the release of adrenocorticotropic hormone (**ACTH**). Adrenocorticotropic hormone, which in turn, activates the adrenal cortical cells to release GC-cortisol and corticosterone (deRoos, 1961; Mikhailova et al., 2007; Madison et al., 2008). Both GCs exert negative feedback on the hypothalamus, helping to return its activity to baseline levels after stimulation (Goncharova et al., 2019; Paul et al., 2022).

Behavioral Responses to Stress

Behavioral responses to stress can be difficult to measure and the interpretation is subjective. Behavioral responses can be affected by various factors such as diurnal variation, genetics, sex, and age making it complex to measure and interpret (reviewed by Marchewka et al., 2013). Differences in an observer's perception of a behavior and ethical values can affect their interpretation of the behavioral observation (Wan et al., 2012; Amici et al., 2019; Grigg et al., 2021). Some researchers have set out to understand the mechanism underlying the behavioral changes in response to stress and ways of using this as an indicator of stress.

Aggressive behavior in animals is influenced by various brain regions and the hypothalamus plays a significant role in its regulation (Roeling et al., 1994). Studies have shown that stimulation of the hypothalamus can lead to the secretion of serotonin also known as 5-hydroxytryptamine (**5-HT**) and dopamine which can trigger aggressive behaviors in rats (Chiavegatto et al., 2001), non-human primates (Seo et al., 2008), humans (Qadeer et al., 2021), and laying hens (Dennis and Cheng, 2011; Huang et al., 2023). Aggression can manifest as feather pecking that can result in injuries and in extreme cases, death (Nicol et al., 1999; Zepp et al., 2018). Stress has been observed as a major causal factor of feather pecking in birds exposed to HS, high stocking density, or isolation (Nicol et al., 1999; Zepp et al., 2018; Davis et al., 2022). Aggression has been shown to increase feed intake and reduce feed conversion ratio in chickens thereby leading to economic loss (Li et al., 2016). Changes in activity, drinking, and feeding patterns have also been associated with stress. For example, a decrease in feed intake and increase in water intake was reported in heat stressed broilers (Rodrigues et al., 2019), laying hens (Kim et al., 2022a), and ducks (Park et al., 2018).

Pecking behaviors in poultry, including feather pecking and cage pecking, may be due to frustration resulting from inability to perform certain behaviors and also in response to elevated temperature (de Haas et al., 2010; Lalonde et al., 2021). Effect of HS on behavior can be validated through administration of exogenous GC which have been reported to increase fear response, anxiety-related behaviors, and an increase in feather pecking (El-lethey et al., 2001; Murray et al., 2008; Mahmoudi et al., 2021). El-lethey et al. (2001) reported that laying hens fed corticosterone and without foraging material developed higher feather pecking rates compared to controls. However, further investigation into the cause of feather pecking is required. Behavior assessments can provide valuable insights into the welfare status of an animal, and it can be combined with other physiological assessments to better understand an animal's welfare status.

Biomarkers of Stress in Poultry

The stress status of an animal can be measured using biological markers. There are 2 main methods of measuring biomarkers of stress in poultry, and these are known as invasive and non-invasive methods (Weimer et al., 2018). Most invasive biomarkers have been validated and are mostly used for assessing stress in poultry however they are subjected to confound from handling stress and blood sampling (Downing and Bryden, 2008; Weimer et al., 2018; Scanes et al., 2020a). The noninvasive method, just as the name implies, is more convenient and less invasive and the validation of this method is on the rise (Weimer et al., 2018; Lee et al., 2022; Oluwagbenga et al., 2022, 2023b). Therefore, validating noninvasive measures for accuracy, reliability and reproducibility would greatly improve the assessment of various stressors in poultry production.

Glucocorticoids in the blood and heterophil to lymphocyte ratio (**HLR**) are considered to be the most commonly measured biomarkers of HS in poultry due to their reliability. Glucocorticoids can be measured in the blood, feces, egg, and feather (Weimer et al., 2018; Bartels et al., 2021; Kim et al., 2021; Lee et al., 2022; Oluwagbenga et al., 2022, 2023b). Although measurement of cortisol as biomarker of stress has been ignored for over 2 decades, recent studies reported an increase in circulating cortisol following exposure to HS or ACTH in poultry thereby showing its importance as an index of stress (Sohail et al., 2010; Kim et al., 2022b; Mirsaiidi Farahani and Hosseinian, 2022; Oluwagbenga et al., 2022; Tetel et al., 2022a,b). ACTH is secreted by the anterior pituitary during stress response therefore it can also be measured as a biomarker of HS (Contarteze et al., 2008; Li et al., 2022). Serotonin turnover rate in the brain is used as an indicator of HS and other form of stressors and this is presented as a ratio of the metabolite, 5HIAA, to serotonin, 5HT (Morgan et al., 1975; Van Hierden et al., 2002; Ahmed-Farid et al., 2021). Other studies reported the measurement of heat shock protein in the blood and tissue (Kang and Shim, 2021; Yu et al., 2021). While most reliable biomarkers have been validated, the level of invasiveness could affect the results, hence the necessity to validate non-invasive biomarkers across different stressors. Therefore, standard protocols should be established for assays and methods used in measuring these biomarkers and periodic review should be published to incorporate advancements.

Glucocorticoids in Blood

Circulating levels of plasma or serum GC is a common biomarker used in evaluating HS and the activation of the HPA axis. This has been validated using synthetic GC such as dexamethasone and ACTH (Weimer et al., 2018; Tetel et al., 2022a; b; Oluwagbenga et al., 2023b). Scanes et al. (2020b) reported a 67.9% increase in plasma corticosterone concentration of turkey treated with ACTH compared with the vehicle-injected birds. Oluwagbenga et al. (2023b) treated Pekin ducks with subcutaneous GC and reported an increase in serum corticosterone and cortisol concentrations. HS, either acute or chronic, has been shown to increase circulating levels of GC in ducks (Oluwagbenga et al., 2022), broilers (Li et al., 2022; Mirsaiidi Farahani and Hosseinian, 2022), and quail (Nassar et al., 2023). Plasma GC levels provide an overview of a bird's stress status at the time the sample was taken therefore there is need for repeated measurement to have a broad idea of stress effect overtime. Repeated handling and blood draws are confounding factors of plasma GC measurement, and this can make interpretation difficult.

Heterophil to Lymphocyte Ratio

Heterophils are a type of granulocytes that are functionally similar to mammalian neutrophils and are important for innate immunity. Lymphocytes are the most common type of white blood cell in birds responsible for controlling the adaptive immune response against pathogens. HS impacts the distribution of heterophils and lymphocytes in the circulation and the ratio between the cell types can be used as a biomarker (Ghasemi and Nari, 2020; Gogoi et al., 2021; Kim et al., 2021; Oluwagbenga et al., 2022; Gil et al., 2023). The study by Gross and Siegel (1983) provided a background for the use of HLR as an indicator of stress in poultry. HLR has been proposed to be a more reliable as an index for acute stress due to the fact HLR response does not change based on the intensity and duration of stressor (Kim et al., 2021; Lee et al., 2022). Proposed reference values for using the HLR as a stress biomarker suggest that values of approximately 0.20, 0.50, and 0.80 indicate low, optimal, and high levels of stress, respectively (Gross and Siegel, 1993). However, HLR should be combined with other physiological parameters when evaluating stress in poultry.

Impact of Heat Stress on Poultry Production

HS can be divided into 2 categories depending on the duration and intensity of the stressor. Acute HS refers to a sudden increase in temperature and humidity over a short period of time while chronic HS occurs when there is a sustained period of high temperature and humidity. In poultry, HS can range from 27°C to 38°C for 1 to 24 h (acute), 7 d (moderate), and more than 7 d (chronic) (reviewed by Vandana et al., 2021). Poultry is known to be most susceptible to HS because of their inability to dissipate heat due to the presence of feather and lack of sweat glands (Zhang et al., 2017). HS has been shown to have negative impacts on the efficiency of poultry production in many studies such as changes in performance, behavioral, and immunological responses. Exposure to chronic HS has been found to lower body weight (Goo et al., 2019), increase feed conversion ratios (Zhang et al., 2017; Welay et al., 2023), and decrease fertility (Oluwagbenga et al., 2022), decrease egg production (Sahin et al., 2002; Mehaisen et al., 2019; Oluwagbenga et al., 2022), meat quality (Lu et al., 2017; Davis et al., 2022), immunity (Hirakawa et al., 2020), egg quality (Ma et al., 2014; Mehaisen et al., 2019), and intestinal barrier dysfunction (Quinteiro-Filho et al., 2010; Qin et al., 2023) in poultry.

Impact of Heat Stress on Production Performance

Several studies have shown that high temperatures can negatively affect the health, physiology, and efficiency of broilers (Quinteiro-Filho et al., 2012; Hosseini-Vashan et al., 2020; Hu et al., 2022; Sun et al., 2023), laying hens (Deng et al., 2012), ducks (Ma et al., 2014; Oluwagbenga et al., 2022), turkeys (Farghly et al., 2017), and Japanese quail (Qin et al., 2023). For instance, Sohail et al. (2012) found that broilers exposed to chronic HS showed reduced feed intake and body weight, and a higher feed consumption ratio. Another study reported the decrease in food intake and increased plasma glucose concentration (Chowdhury et al., 2012). Chronic HS can also disrupt fat metabolism, reduce muscle growth, and negatively impact the quality and nutrient composition of meat (Dai et al., 2012; Al-Sagan et al., 2020). In addition, high ambient temperatures can lead to higher mortality rates and welfare issues, reduced feed intake and egg production in laying hens (Ebeid et al., 2012; Vecerek et al., 2016; Caffrey et al., 2017). The effects of HS on poultry may vary depending on the duration and intensity of the stress, age and physiological status, sex, and their genetic potential.

Impact of Heat Stress on Female Reproduction

The negative feedback mechanism of GC on the hypothalamus and anterior pituitary during HS can lead to a decrease in the secretion of the gonadotropin-releasing hormone (**GnRH**) in the hypothalamus. This can in turn impair the secretion of follicle-stimulating hormone (**FSH**) and luteinizing hormone (**LH**) from the pituitary gland (Jeronen et al., 1978; Li et al., 2020b; Zhang et al., 2022). These changes in gonadotropin secretion can cause the ovary to regress, impair steroidogenesis, and thereby lead to a decrease in reproductive efficiency (You et al., 1995; Rozenboim et al., 2007). Heat stress can also directly affect ovarian function by reducing blood flow to the ovary, leading to decreased ovarian weight and number (Wolfenson et al., 1981; Rozenboim et al., 2007; Oluwagbenga et al., 2022). Another study reported that HS caused oocyte apoptosis by inhibiting the proliferation of granulosa cells and a decrease in the secretion of estrogen and progesterone (Luo et al., 2016; Li et al., 2020a). These effects are evidenced by reduced egg production in laying hens exposed to HS.

HS can impair performance and production of laying hens by causing a decline in egg production and quality. Rozenboim et al. (2007) exposed White Leghorns to high temperatures and their results showed a reduction in egg production, egg weight, ovarian weight, and the number of large follicles. Heat-exposed ducks showed lower egg production and reduced oviduct weight and length, and the number of matured ovarian follicles (Ma et al., 2014; Oluwagbenga et al., 2022). Other studies on laying hens showed similar results, egg production and quality were significantly depressed in heat-stressed hens (Mashaly et al., 2004; Rubio et al., 2021). When hens are subjected to HS, their feed intake decreases, which affects the availability of nutrients and leads to the lower egg production and quality (Mashaly et al., 2004; Mazzoni et al., 2022). Additionally, heat exposure can disrupt calcium metabolism and decrease the concentration of calcium in the plasma, leading to thinner eggshells and a higher number of eggs with cracks or breaks (El-Tarabany, 2016; Cruvinel et al., 2021). In addition, HS may lower the reproductive efficiency of hens at the hypothalamus and pituitary gland level or by directly impacting the ovary (Rozenboim et al., 2007; Li et al., 2020a,b). The reduction in egg production caused by exposure to HS was shown by another study to be caused by follicular apoptosis (Li et al., 2020a).

Administration of ACTH or GC has been reported to impair egg production. A study exposed laying hens to different doses of ACTH injection and egg production ceased in the hens that received ACTH 40 and 80 IU (Flickinger, 1966). The authors further reported that hens injected with 80 IU ACTH showed ovarian atrophy. Further, oral corticosterone delayed the onset of lay and decreased egg production of brown layers (Shini et al., 2009). Laying hens fed diet containing corticosterone showed a decrease in egg production and delayed start of lay (El-lethey et al., 2001). Egg weight and percentage egg laid was significantly decreased in Japanese quail exposed to exogenous corticosterone through drinking water (Wall and Cockrem, 2010). The melanocortin 2 receptor (MC2R) is the main ACTH receptor in the adrenal gland, where they control GC and mineralocorticoid (MC) production (Nimura et al., 2006; reviewed by Mountjoy, 2010). ACTH also have extra adrenal functions and MC2R mRNA has been found in the brain and blood cells of mice and brain of fish (Klovins et al., 2004; Nimura et al., 2006). In addition, MC2R is also expressed in the ovaries and testes of rainbow trout fish (Aluru and Vijayan 2008) and in bovine ovary (Etchevers et al., 2021). Therefore, the effect of ACTH on egg production may be mediated through its receptors in the ovaries; however, there is need for further research to confirm this prospect in birds.

HS can cause a significant economic loss by causing up to 15.8% decrease in egg quality (Song et al., 2012). The 2 main qualities that are measured during egg quality assessment include external qualities such as egg weight and shell condition while internal qualities consist of albumen height and yolk weight (2000). El-Tarabany (2016), showed that HS decreased both external egg quality parameters and internal egg quality parameters in Japanese quail. Another study reported a decrease in egg weight of Japanese quail following exposure to cyclic HS (Vercese et al., 2012). Various studies have reported a decreased in egg quality of laying ducks (Sahin and Kucuk, 2003; Ma et al., 2014; Luo et al., 2018; Oluwagbenga et al., 2022) and chickens (Mashaly et al., 2004; Ebeid et al., 2012; Kim et al., 2020, 2022a) following exposure to HS.

There are several factors responsible for the decreased shell quality observed in hens exposed to HS one of which may be due to reduced plasma calcium level (El-Tarabany, 2016; Kim et al., 2020). Exposure to high temperatures decreased plasma calcium levels and the uptake of calcium by duodenal cells, leading to a decrease in the availability of calcium for shell formation (Mahmoud et al., 1996; Kim et al., 2020). Additionally, high temperatures have been shown to stimulate bone resorption, leading to an excess of phosphorus in the blood that hinders the deposition of calcium in the shell gland (El-Tarabany, 2016). One of the responses to HS is panting that can decrease the blood carbon dioxide level needed for the formation of calcium carbonate required for shell formation (El-Tarabany, 2016; Kim et al., 2021). Calcium-binding protein, also known as calbindin, exists in 2 forms and is found in various tissues in mammals and birds (de Moraes et al., 2021). High concentrations of calbindin are found in avian tissues with high levels of calcium transport, such as the intestine and eggshell gland (Sugiyama et al., 2010; de Moraes et al., 2021). Calbindin facilitates calcium transport; therefore, it determines the rate of calcium deposition during egg formation (Bar et al., 1992). Studies have shown that HS decreases the calbindin intensity thereby impairing transport and absorption of calcium (Franco-Jimenez and Beck, 2007; Ebeid et al., 2012; de Moraes et al., 2021). These results validate the detrimental effects of HS on egg production and quality. However, the mechanism by which ACTH and GC affect egg quality is not fully established.

Impact of Heat Stress on Male Reproduction

Some studies have reported conflicting effects of HS on sperm characteristics (Wang et al., 2014, 2018; Shanmugam et al., 2015). In one study, male broiler breeders exposed to a temperature of 27°C showed 48% decrease in in vivo sperm penetration compared to males maintained at 21°C (Mcdaniel et al., 1996). In other studies, sperm from heat-stressed roosters showed reduced longevity within the sperm storage tubules in the female reproductive tract, altered gene expression, and increased apoptosis (King et al., 2002; Wang et al., 2014). Sertoli cells in the testes are important for the growth and development of germ cells. However, HS may negatively impact Sertoli cells by decreasing FSH (stimulates the Sertoli cells to secrete androgen binding protein that binds testosterone) thereby impairing spermatogenesis (Guo et al., 2021). Heat stress may decrease sperm quality by causing a decrease in semen volume and testes weight, as well as reduced sperm concentration, motility, and viability (Guo et al., 2021; Rao Telangana et al., 2021). Heat stress can also impact sperm quality by reducing androgenic receptors and spermatogenic cell counts (Türk et al., 2016) and DNA damage in sperm cells (Hou et al., 2015). Exposure to HS during embryonic development may promote testicular growth and sperm quality while most detrimental effects are seen in exposure at later stage of life (Shanmugam et al., 2015).

Impact of Heat Stress on Immunity

The avian immune system comprises innate immunity which provides the first line of defense and adaptive immunity and consists of the T and B cells (reviewed by Davison, 2022). T cells and B cells provide an immune response against antigens through cell-mediated and humoral responses, respectively (Hirakawa et al., 2020). B cells are antibody producing cells and the 3 types of antibodies in birds include immunoglobin M, A, and G (Liu et al., 2019). The bursa of Fabricius and the thymus are essential for the development and maturation of lymphocytes and can be impacted by HS (Al-Ogaili and Hameed, 2021). In poultry, the weights and relative weights of the thymus, bursa, and spleen are commonly used as indicators of immune function (Walkden-Brown et al., 2013; Goel et al., 2017). While the weight of an organ can be a quick way to assess immune function, it is not always a reliable indicator of the actual immune changes occurring within the organ (Walkden-Brown et al., 2013).

HS can dampen the immune response of poultry by reducing the weights and function of immune organs such as spleen, thymus, and bursa (Niu et al., 2009; Hirakawa et al., 2020; Hosseini-Vashan et al., 2020). HS was reported to cause morphological damage to thymus and bursa, and the depression of cells essential for the proliferation of B cells in the spleen of broilers (Hirakawa et al., 2020; Liu et al., 2021). The authors further stated that plasma titer of antibodies such as immunoglobin Y, M, and A were lower than the thermoneutral. In another study, HS was reported to reduce the relative weights of spleen, bursa, and thymus in broilers (Quinteiro-Filho et al., 2010; Hosseini-Vashan et al., 2020; Hu et al., 2022). In broilers, HS was reported to reduce the lymphoid organ weight, antibody responses and phagocytic ability of macrophages (Niu et al., 2009; Hirakawa et al., 2020).

Circulating catecholamine levels increase during HS and can promote the production of cytokines that can lead to a hyperactive immune system (Li et al., 2022). GCs can cause immunosuppression by depressing immune cells such as macrophages, mast cells, and basophils (Su et al., 2021), reduction in white blood cells and levels of inflammatory cytokines (Niu et al., 2009; Ju et al., 2014), and reduction in certain immune cells such as T cells (Xiang-hong et al., 2011; Huo et al., 2019). These results show that HS can increase the susceptibility of a flock to disease outbreak and the implication of this is high mortality rate and compromise of food safety and public health.

The Bursa of Fabricius

The bursa of Fabricius is small sac-like organ located in the cloaca and is an essential immune organ for producing humoral immunity (Bagheri et al., 2022). Bursa is a site for antigen exposure and production of B cell receptors and is capable of transferring antigens and antibodies into circulation (Cazaban et al., 2015). Maturation and differentiation of lymphocytes take place in the bursa which are mostly B cells and to a lesser extent T cells (Dolfi et al., 1989; Li et al., 2015). Antibody levels are correlated with the size of bursa, which is indicative of a bird's immune capacity and overall health (Mueller et al., 1962; Sadler and Glick, 1962). Bursa size varies with age reaching maximum size at 8 to 10 wk followed by progressive regression (Fang and Peng, 2014; Raji et al., 2017). Cazaban et al. (2015) proposed a minimum bursa size relative to body weight for broilers between 1 and 6 wk to be 0.11 g/kg. Therefore, there is a need to establish standards for other poultry species and revise the previous standard to reflect differences in genetics.

Stress can lead to reduction in size and function of the bursa and the change in size can be used as an index of stress in poultry. HS has been shown to lead to a reduction in the bursa weight and function in broilers (He et al., 2019; Hosseini-Vashan et al., 2020; Sun et al., 2023). Another study in broiler showed that HS increased the apoptosis rate and elevated the concentration of cytokines in the bursa (Tarek et al., 2013; Liu et al., 2021). The effects of HS on the bursa can be validated by the administration of ACTH and GC which have been reported to reduce the size and function of the bursa in a dose dependent manner (Siegel and Beane, 1961; Davison et al., 1985; Puvadolpirod and Thaxton, 2000). The bursa of Fabricius was investigated for its steroidogenic enzymes, revealing that this organ produces cortisol through its steroidogenic pathways (Lechner et al., 2001; Schmidt et al., 2009; Taves et al., 2016). Additionally, other studies pointed out that cortisol binds more strongly to the GC receptors in the bursa of chickens compared to corticosterone (Lechner et al., 2001; Schmidt et al., 2010). In addition to circulating cortisol, shrinkage in the size of bursa might be a result of the paracrine effect caused by cortisol secreted by the bursa. Bursa size varies based on the type and intensity of stressor and the dose and duration of exposure to ACTH and GC. Finally, bursa size with other indicators of immune response can be used to evaluate HS and immune status of poultry although this is limited to young birds. Other factors such as disease and vaccination status can also affect bursa size (Cazaban et al., 2015; Raji et al., 2017), therefore there is need to consider these factors when interpreting results.

Spleen

The spleen is an important immune organ that consists of red pulp that filters out pathogens, damaged red blood cells and is involved in red blood cell production. The splenic white pulp contains areas for T and B cells (Erf et al., 1998; Khalil et al., 2009; Tarek et al., 2018). Poultry have a less developed lymphatic system compared to mammals and rely on the spleen for immunity. There are individual differences in spleen weights, but the spleen tends to grow rapidly and peak around first 6 wk in broiler chickens (Tarek et al., 2018). Heat stress has also been reported to cause a decrease in spleen weight and splenic cytokines (Ohtsu et al., 2015) and an increase in spleen apoptosis rate in broilers chicken (Liu et al., 2022). However, Adu-Asiamah et al. (2021) reported a strain difference in the effect of HS on splenic cytokines in 2 local strains of chicken. Heat stress resulted in decreased splenic B and T cells and an underdeveloped germinal center thereby leading to the depression of B cell proliferation in broilers (Hirakawa et al., 2020). Other studies also reported a decrease in relative spleen weight following exposure to HS in broilers (Ghazi et al., 2012; Chand et al., 2014; Liu et al., 2014; He et al., 2019), and laying hens (Attia et al., 2016). The effects of HS on spleen weight can also be validated through ACTH or GC administration that have been reported to cause spleen shrinkage (Mumma et al., 2006; Shini et al., 2009). A study reported a decrease in relative spleen weights in chickens exposed to ACTH at 8 IU/kg/d for 7 d (Puvadolpirod and Thaxton, 2000). Chicks injected with lipopolysaccharide to stimulate an immune reaction showed an increase in spleen weights over 48 to 72 h showing a correlation between spleen weight and immune activity (Cheng et al., 2004). Chickens with larger spleen weight have been found to have a stronger immune response (Felver-Gant et al., 2012). Therefore, spleen weight relative to body weight may be a useful indicator of poultry's stress status and their ability to adapt to stressors.

Thymus

The thymus is a gland located in the neck of birds and the number reported by different studies are within the range of minimum of 6 and maximum of 9 lobes of different sizes and shapes on each side of the neck (Tarek et al., 2012; Haseeb et al., 2014; Huralska et al., 2020). The lobes are made up of a central medulla surrounded by a cortex; both are involved in the development of T cells. The thymus reaches maximum size around 2 wk of age and begins to involute around 7 wk of age in broiler chickens (Tarek et al., 2012). HS has also been reported to promote the involution of the thymus in exposed birds (Anwar et al., 2004; He et al., 2019) while another study reported no change (Liu et al., 2014). Further, damage to the thymic cortex was reported in broiler chickens exposed to HS thereby leading to the depression of T cell maturation (Hirakawa et al., 2020). Similar to the bursa and spleen, the thymus also tends to shrink in size in response to the administration of ACTH or GC with no reversion after treatment was stopped (Puvadolpirod and Thaxton, 2000; Gomez-Sanchez, 2009). In contrast, Glick (1967) reported a regression in the thymus weight of chicks injected with ACTH for the first 5 d after hatching but recovered when examined at 3 and 6 wk of age. This disparity might be a result of differences in age, dosage and duration of ACTH administered. Thymus is capable of producing cortisol which binds with high affinity to GC receptors in the thymus therefore mediating a paracrine effect (Lechner et al., 2001; Schmidt et al., 2009) and this might impact thymus size, proliferation and T-cell development. In summary, the thymus might be a useful indicator of a chicken's immune strength and stress status, however, interpretation should be made in relation to the species, age, type and intensity of the stressor.

Hormone-Mediated Maternal Effect

The environmental condition experienced by the mother during fetal development in mammals or during egg formation in birds can lead to the modification of the offspring phenotype (reviewed by Groothuis et al., 2019). Hormone mediated maternal effect is the transfer of nutrients or steroid hormones from the mother to the fetus or egg which in turn modifies the offspring phenotype (Henriksen et al., 2011; Pu et al., 2019; Peixoto et al., 2020a). Hormones in egg can lead to changes in phenotype which influences physiology, behavior, and morphology (Peixoto et al., 2020a; Oluwagbenga et al., 2023a). GC deposition in egg has been reported (Love et al., 2008; Okuliarová et al., 2010; Caulfield and Padula, 2020; Engel et al., 2022; Oluwagbenga et al., 2023b) and an increase in deposition has been reported following HS in laying hens (Downing and Bryden, 2008; Kim et al., 2022a), Japanese quails (Pu et al., 2019, 2020), and ducks (Oluwagbenga et al., 2022).

GC levels in the egg may indicate maternal conditions in terms of age, welfare, and environment and this can alter both pre-hatch and post-hatch welfare and development. Maternal GC can be deposited in either albumen, yolk or both (Hayward and Wingfield, 2004; Pu et al., 2019; Caulfield and Padula, 2020). The potential of GC as a mediator of maternal effect on offspring can be validated through in ovo administration of GC into the albumen or yolk, or through subcutaneous implantation, oral or intravenous administration of GC into the hen (Henriksen et al., 2011; Bowers et al., 2016; Oluwagbenga et al., 2023b). Several studies have reported the effect of in ovo administration of corticosterone on embryonic and posthatch development of the offspring. Some of these effects include reduced hatchability, lower hatching and posthatch body weight, reduced competitive ability, lower posthatch growth rate, increase embryo mortality and higher fearfulness (Saino et al., 2005; Janczak et al., 2006, 2007; Eriksen et al., 2010; Peixoto et al., 2020a,b; Oluwagbenga et al., 2023a). Hayward and Wingfield (2004) reported a decrease in hatching weight, growth rate, and GC secretion in response to restraint stress in the offspring of Japanese quail implanted with corticosterone.

Maternal exposure to HS has been shown to modify the offspring's phenotype. Oluwagbenga et al. (2023a) reported a significant increase in HPA activity, HLR, and fearful behavior in the offspring of heat-stressed Pekin ducks. Japanese quail from heat stressed parent showed lower performance and high protein oxidation in response to heat stress compared to those from parents exposed to thermoneutral condition (Santana et al., 2021). Further, higher inflammatory and lower antibody responses were reported in Japanese quails from parent exposed to chronic HS (Videla et al., 2020). In a comprehensive study, parent exposure to high temperature resulted in lower body weight, feed intake, and meat yield in broilers (Zhu et al., 2017). Although the maternal effect of heat stress on offspring development has garnered considerable attention in mammalian studies, there are limited studies in poultry leaving a substantial gap in the comprehension of this topic. By understanding the mechanisms underlying GC-mediated modification of phenotype, it would be possible to use maternal hormones as a tool to produce offspring that are better able to handle stress. Much more research concerning the potential epigenetics of heat stress events, or compounded heat stress events, is necessary to better understand how we need to alter management or genetics in order to better handle global climate changes.

CONCLUSION AND RECOMMENDATIONS

Heat stress poses a significant threat to the poultry industry, and this concern will intensify as climate change continues to elevate environmental temperatures. Extensive research conducted across multiple studies examined in this review consistently demonstrates that HS negatively impacts various aspects of poultry production, including production performance, egg production, egg quality, meat quality, reproductive performance, and overall welfare. The detrimental effects of HS on production performance in poultry cannot be overlooked. Therefore, addressing the impact of HS on poultry production necessitates the development and implementation of appropriate strategies that adopt a multifaceted approach for a comprehensive solution. Environmental strategies focused on enhancing management practices, such as optimizing ventilation systems, poultry house designs, and adjusting stocking density, can effectively alleviate the negative effects of HS. These measures aim to improve air circulation and thermal comfort within poultry housing, thereby mitigating the heat load on birds. In addition to environmental strategies, genetic approaches offer great potential for long-term solutions to counteract the adverse effects of climate change on poultry. Genetic selection programs can be employed to develop poultry breeds with enhanced tolerance to HS without compromising growth performance and welfare. By selectively breeding for heat-tolerant traits, such as improved thermoregulation, reduced metabolic heat production, and enhanced resilience to oxidative stress, poultry can better adapt to challenging HS conditions.

In recent times, early-life thermal conditioning and epigenetic modifications have emerged as potential strategies for mitigating the detrimental effects of HS in poultry. Early-life thermal conditioning involves subjecting chicks to sublethal HS during their early developmental stages, which triggers physiological and molecular adaptations that enhance their resilience to subsequent heat exposure. Additionally, epigenetic modifications, which refer to alterations in gene expression patterns without changes to the underlying DNA sequence, have shown promise in modulating the response of poultry to HS through the selection for epigenetic markers for high heat tolerance. Recent study has shown that early thermal conditioning help reduce heat production in young chickens (Ouchi et al., 2021b). Other studies reported that early thermal conditioning altered DNA methylation in the brains of chickens (Ouchi et al., 2021a), decreased plasma corticosterone levels, heat shock proteins, and antioxidant enzyme gene expressions (Madkour et al., 2021). Further, a decrease in respiratory rate in response to HS, reduction in thyrotropin releasing hormone, and lower corticotropin releasing hormone was reported in chicks exposed to either early or late thermal conditioning (Ouchi et al., 2020). Further, HS increased the methylation of histone H3 lysine 27 in the adrenal gland of chickens, a modification linked to the regulation of adrenal glands endocrine activities, which may contribute to thermotolerance (Zheng et al., 2021). These research findings showed that early thermal conditioning and the resulting epigenetics modification may improve thermotolerance of poultry. However, there is need for future research in investigating the long-term effects, unraveling underlying mechanisms, and optimizing protocols are essential steps to fully harness the benefits of these approaches.

DISCLOSURES

The authors do not declare any conflicts of interest.

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