Heat Stress on Meat Quality Status

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Heat stress is one of the most stressful events in livestock life, negatively impacting animal health, productivity, and product quality.

Keywords: heat stress ; meat quality ; product ; muscle glycogenolysis

1. Introduction

Food quality is a very complex and broad concept that has changed rapidly in recent years. Recently, it has represented the set of all food properties that are closely related to physicochemical properties, texture, and taste that are acceptable and satisfying to consumers. Previous studies showed that consumers' concerns about food quality have been increasing, in recent decades, particularly concerning the perceived healthiness of food [1][2][3]. Meat and various meat products are important sources of high-quality proteins, fats, and minerals as essential nutrients [4][5]. As animal welfare concerns grow and consumers become more conscious of food quality, there is an increasing focus on improving the quality, safety, and nutritional value of meat. Based on current knowledge, increasing global warming and climate change appear to pose a potential threat to food security in the coming decades [6][7]. Heat stress (HS) is one of the major impacts of climate change (CC) on livestock raised in both intensive and extensive production systems [8]. This is especially true given its negative impact on behavior, immune response, gut integrity, productivity, and meat quality [9]. Heat stress is a form of hyperthermia (elevated body temperature) in which the body's physiological systems are unable to regulate body temperature within normal limits [8]. It is well known that, at temperatures higher than an animal's thermoneutral zone, heat stress can affect animal welfare, performance, and product quality.

2. Heat Stress and Carcass Characteristics

Carcass and meat quality depend on both intrinsic and extrinsic factors. The intrinsic factors include species, breed, gender, age, and slaughter weight. The extrinsic factors include weaning, diet, and stress [10][11]. This latter can be attributed to the breeding conditions, the transport, or the environment. To maintain euthermia, heat-stressed animals activate some physiologic and metabolic adjustments at the expense of growth, reproductive, and productive aspects [12][13]. For this purpose, homeothermic animals reduce their feed intake to lower metabolic heat production [14]. However, such an adaptive response has implications on carcass characteristics in monogastric and ruminants as well. Carcass yield, carcass fat deposition, and intramuscular fat content were reported to be decreased in poultry [15][16], pigs [17][18], sheep [19], goats [20], and cattle [19][21]. A reduction in subcutaneous fat was also reported in pigs subjected to chronic HS, to enhance heat dissipation [22]. Holinger et al. [23] described that the carcass of heat-stressed pigs had reduced lean meat percentage and thicker backfat. The extent of changes indeed depends on the species, but it is known that the economic losses caused by carcass yield loss are great [24]. At the same time as fat content dropped, acetyl coenzyme A carboxylase enzyme, L (+) P-hydroxy acyl CoA dehydrogenase, and lipolytic enzyme activities were decreased [17][22]. Pearce et al. [17] demonstrated that this decrease is independent of heat stress-induced reductions in feed intake. Nevertheless, no significant effects on intramuscular fat were reported in broilers subjected to heat stress for 3 weeks [25] and heat-stressed goats for 1 month [11]. Similarly, Mader et al. [26] and Ponnampalam et al. [27] did not report any significant difference between chronic heat stress (1 week) and thermal neutral groups in subcutaneous fat in cattle and carcass fat scores in lambs. These findings may be attributed to the ability of the breeds to cope with heat stress conditions, and to the duration and severity of HS [11]. However, it is noteworthy to mention that although the carcass weight was significantly affected by heat stress-induced feed intake reduction, the impacts on carcass composition are confusing and need further investigation.

3. Heat Stress and Rapid pH Drop

After slaughter, skeletal muscle undergoes physical structural, and biochemical changes. These changes are triggered by the cession of blood flow and oxygen supply, and the scarcity of glucose resources. Under these conditions, and for postmortem homeostasis purposes, skeletal muscle metabolizes stored glycogen for adenosine triphosphate (ATP) synthesis and use [28]. Lactic acid and hydrogen ions (H^+) are the endeavor products of several chemical reactions leading to the conversion of glycogen to lactic acid [15]. Since oxygen is lacking, the electron chain is interrupted and pyruvate can no longer enter the mitochondria [28][29]. Hence, lactic acid and H^+ accumulate, resulting in pH lowering [30]. pH is widely recognized as one of the most accepted indicators of meat quality. Any homeostatic disturbance of postmortem metabolism (e.g., such as rapid pH drop and lower pHu) leads to meat quality defects such as pale, soft, and exudative (PSE) meat, high ultimate pH (pHu) meat (dark, firm, and dry (DFD) meat) and dark-cutting in ruminants [30]. Several studies associated heat stress with a high glycolysis rate and rapid pH decline, resulting in serious damage to skeletal muscle. In broilers under short-term heat stress (36 °C, 1 h), AMP-activated protein kinase (AMPk) activity at 1 h postmortem was greater than that of broilers under thermal neutral (25 °C) conditions [31]. This was also the case with broilers exposed to chronic HS [32]. Moreover, broilers transported during summer (32–42 °C) registered a higher adenosine monophosphate/adenosine triphosphate (AMP/ATP) ratio, increased AMPK, and lower pHu value [33][34]. It is worth noticing that some authors did not register any significant decline in ultimate pH muscle in broilers [35][36].

During and after slaughtering, HS stimulates anaerobic glycolysis within the muscles. The hydrolysis of ATP governed primarily by pyruvate kinase and lactate dehydrogenase in anaerobic conditions then escalates. More pyruvate is converted to lactate leading to an accumulation of H^+ and lactic acid [37][38]. The result is a rapid pH drop which lowers the water-holding capacity and is at the origin of PSE meat [39][40]. In ruminants, heat stress results in pHu values greater than 5.8, a normal pHu muscle value [41][42]. This finding may be attributed to the effect of the cortisol hormone, which increases under HS conditions. As a result, antemortem skeletal muscle glycogen content is noteworthy reduced and postmortem glycolytic enzyme activity is enhanced [42]. Contrarily, in chickens, heat stress does not affect the antemortem glycogen content [35]. Postmortem glycolytic enzyme activity and pH drops are then faster and greater. Interestingly, some authors demonstrated that high ambient temperature and/or long-term heat exposure may not necessarily have adverse effects on muscle pH and meat quality [33][43]. This could be explained by animals' adaptation to heat stress [43]. However, rapid pH drops and meat quality damage seem to be associated with short-term exposure to acute ambient temperatures [40][42].

4. Meat Color and Water Holding Capacity

Besides its detrimental effects on feed intake and growth rate, heat stress was reported to impact physicochemical properties such as color, texture, WHC, and organoleptic properties such as softness, consistency, flavor, and odor in chicken and pork [44][45][46]. Protein denaturation is a result of HS exposure before slaughtering. As proteins are involved in the WHC of meat, each protein damage impedes its ability to bind water. The cumulative effect leads to an impaired WHC marked by high drip and cooking loss [47]. In this trend, numerous studies reported increased values of heat loss and shear force in heat-stressed meat-type broilers [15].

In chickens and pigs, muscles consist of fast-twitching fibers [39][40]. These fibers rely mainly on anaerobic glycolysis [48]. Exposure to stressful ambient temperatures before slaughtering allows for augmented carcass temperature [49], accelerated glycolysis rate, increased H^+ and lactic acid levels, and elevated protein degradation rate. Consequently, PSE conditions are developed [50]. PSE meat is poorly processed meat, more dry and brittle, and has a poor texture, higher lightness, and lower sensory score [37][39][51] due to its hindered WHC and protein extractability [52][53]. In ruminants, increased pHu values under heat stress conditions negatively affect the shrinkage of the myofilament lattice leading to darker meat color. Many meat quality defects were reported, including higher light absorption, less light scattering, higher oxygen consumption, lower WHC, and increased toughness [41][45][54][55]. However, it seems that these meat quality attributes may be influenced by the duration of heat stress exposure, and the extent of the ambient temperature [27][33][56].

5. Impacts of Heat Stress on Muscle Biochemical and Chemical Properties

It is known that ruminants, pigs, and poultry are highly vulnerable to HS due to their rapid metabolism and growth, high production, and species-specific characteristics such as rumen fermentation, transpiration, and skin insulation [57]. Numerous studies have documented how HS affects muscles [58][59]. According to Sula et al. [60], HS results in myocyte fibers that are homogenously eosinophilic, hypereosinophilic, and fragmented. It has been reported that chronic HS would increase the production of lactate in muscle and affect the meat quality. Therefore, acute HS before slaughter accelerates muscle glycogenolysis and increases lactate concentrations in early postmortem slaughter while carcasses are still warm

[53]. The result is PSE meat characterized by a decreased WHC, jointly reported in poultry [61][62], but also found recently in cattle [63][64]. Contrarily, animals under chronic HS have diminished muscle glycogen stores, leading to lower lactic acid generation, leading to DFD meat with a higher ultimate pH in ruminants [65], but also in pigs [66]. Additionally, HS effects primarily involve autonomic responses due to the activation of the autonomic nervous system (ANS), which is regulated by catecholamines (adrenaline and norepinephrine) (**Table 1**). This includes increased respiration and heart rate, increased body temperature, and the redistribution of blood flow from the intestine to the skin for thermoregulation, hence energy utilization from body stores [67] promotes muscle glycogenolysis and inhibits energy storage [65][68]. Both acute and chronic HS cause increases in plasma glucocorticoid concentrations via the activation of the hypothalamic–pituitary–adrenal (HPA) axis. Nevertheless, acute HS leads to increased glucocorticoids more than chronic HS [69]. Glucocorticoids enhance heat loss through vasodilation [70] and increase proteolysis and altered lipid metabolism; proteolysis occurs because of an increased rate of myofibrillar protein degradation in skeletal muscle as mediated by the following mechanisms: the Ca^{2+}-dependent-ubiquitin–proteasome, and autophagy–lysosome system [71][72][73] (**Table 1**).

HS stimulates the hypothalamic–pituitary–adrenal system in poultry, increases the concentration of the circulating hormone corticosterone [74], and has profound effects on protein and lipid metabolism, body composition, and meat quality [75]. Imiku et al. [16] and Lu et al. [76] provided evidence that HS is associated with chemical alterations in chicken meat. High levels of the hormone corticosterone (glucocorticoid) increase fat accumulation in the abdomen, neck, and thighs [77][78][79], but boosted protein degradation and skeletal muscle breakdown [75], potentially via the expression of fatty acid transport protein and the insulin receptor in the pectoralis major [79]. The exposure of animals to HS is related to an elevation in the expression of heat shock proteins in ruminants and pigs [12][80][81], most notably the small alpha βcrystallin (αβC) heat shock protein (sHSP). Heat shock proteins are key components of living muscle that regulate the cytoskeleton and control cell maintenance [82].

In rabbits, HS affects the amount of myoglobin in the muscle, which leads to a decrease in the pigment content of the meat [83].

Table 1. Effects of heat stress on biochemical and chemical parameters of the muscle.

Origin	Chemical Class	Sub-Class	References
Pigs	**Steroid hormones**	**Glucocorticoids**	[70]
	Carbohydrates	**Glycogen**	[62]
	Organic acid	**Lactic acid**	[53]
Ruminants	**Protein**	**Myofibrillar protein**	[72]
		alpha βcrystallin (αβC) heat shock protein (sHSP) and HSP27	[12][80][81]
	Steroid hormones	**Glucocorticoids**	[70]
	Organic acid	**Lactic acid**	
	Carbohydrates	**Glycogen**	[62]
	Lipid	**Volatile fatty acids**	
Broiler	**Hormone**	**Corticosterone**	[74]
		Insulin	[79]
	Protein	**alpha βcrystallin (αβC) heat shock protein (sHSP) and HSP27**	[12][78][80][81]
	Organic acid	**Lactic acid**	[54]
	Steroid hormones	**Glucocorticoids**	[70]
	Lipid	**Fatty acid**	[78]
Rabbit	**Organic acid**	**Lactic acid**	[4]
	Lipids	**-**	[84]
	Proteins	**-**	[84]
	Metalloprotein	**Myoglobin**	[83]

References

1. Teixeira, A.; Rodrigues, S. Consumer perceptions towards healthier meat products. Curr. Opin. Food Sci. 2020, 38, 147–154.
2. Baba, Y.; Kallas, Z.; Costa-Font, M.; Gil, J.M.; Realini, C.E. Impact of hedonic evaluation on consumers' preferences for beef attributes including its enrichment with n-3 and CLA fatty acids. Meat Sci. 2016, 111, 9–17.
3. Hung, Y.; de Kok, T.M.; Verbeke, W. Consumer attitude and purchase intention towards processed meat products with natural compounds and a reduced level of nitrite. Meat Sci. 2016, 121, 119–126.
4. Kurćubić, V.; Stajić, S.; Miletić, N.; Stanišić, N. Healthier Meat Products Are Fashionable-Consumers Love Fashion. Appl. Sci. 2022, 12, 10129.
5. Aminzare, M.; Aliakbarlu, J.; Tajik, H. The effect of Cinnamomum zeylanicum essential oil on chemical characteristics of Lyoner-type sausage during refrigerated storage. Vet. Res. 2015, 6, 31.
6. Chauhan, S.S.; Dunshea, F.R.; Plozza, T.E.; Hopkins, D.L.; Ponnampalam, E.N. The Impact of Antioxidant Supplementation and Heat Stress on Carcass Characteristics, Muscle Nutritional Profile and Functionality of Lamb Meat. Animals 2020, 10, 1286.
7. FAO; IFAD; UNICEF; WFP; WHO. The State of Food Security and Nutrition in the World 2018: Building Climate Resilience for Food Security and Nutrition; FAO: Rome, Italy, 2018.
8. Thornton, P.; Nelson, G.; Mayberry, D.; Herrero, M. Impacts of heat stress on global cattle production during the 21st century: A modelling study. Lancet Planet. Health 2022, 6, 192–201.
9. Lara, L.J.; Rostagno, M.H. Impact of Heat Stress on Poultry Production. Animals 2013, 3, 356–369.
10. Guerrero, A.; Valero, M.V.; Campo, M.M.; Sañudo, C. Some Factors That Affect Ruminant Meat Quality: From the Farm to the Fork. Review. Acta Sci. 2013, 35, 335–347.
11. Archana, P.R.; Sejian, V.; Ruban, W.; Bagath, M.; Krishnan, G.; Aleena, J.; Manjunathareddy, G.B.; Beena, V.; Bhatta, R. Comparative assessment of heat stress-induced changes in carcass traits, plasma leptin profile and skeletal muscle myostatin and HSP70 gene expression patterns between indigenous Osmanabadi and Salem Black goat breeds. Meat Sci. 2018, 141, 66–80.
12. Baumgard, L.H.; Rhoads, R.P. Effects of heat stress on postabsorptive metabolism and energetics. Ann. Rev. Anim. Biosci. 2013, 1, 311–337.
13. Rhoads, R.P.; Baumgard, L.H.; Suagee, J.K. Early Careers Achievement Awards: Metabolic priorities during heat stress with an emphasis on skeletal muscle. J. Anim. Sci. 2013, 91, 2492–2503.
14. Marai, I.F.M.; El-Darawany, A.A.; Fadiel, A.; Abdel-Hafez, M.A.M. Physiological traits as affected by heat stress in sheep—A review. Small Rumin. Res. 2007, 71, 1–12.
15. Zhang, Z.Y.; Jia, G.Q.; Zuo, J.J.; Zhang, Y.; Lei, J.; Ren, L.; Feng, D.Y. Effects of constant and cyclic heat stress on muscle metabolism and meat quality of broiler breast fillet and thigh meat. Poult. Sci. 2012, 91, 2931–2937.
16. Imik, H.; Ozlu, H.; Gumus, R.; Atasever, M.A.; Urcarand, S.; Atasever, M. Effects of ascorbic acid and a-lipoic acid on performance and meat quality of broilers subjected to heat stress. Br. Poult. Sci. 2012, 53, 800–808.
17. Pearce, S.C.; Upah, N.C.; Harris, A.; Gabler, N.K.; Ross, J.W.; Rhoads, R.P.; Baumgard, L.H. Effects of heat stress on energetic metabolism in growing pigs. Faseb J. 2011, 25, 1052.
18. Spencer, J.D.; Boyd, R.D.; Cabrera, R.; Allee, G.L. Early weaning to reduce tissue mobilization in lactating sows and milk supplementation to enhance pig weaning weight during extreme heat stress. J. Anim. Sci. 2003, 81, 2041–2052.
19. Maloiy, G.M.; Kanui, T.I.; Towett, P.K.; Wambugu, S.N.; Miaron, J.O.; Wanyoike, M.M. Effects of dehydration and heat stress on food intake and dry matter digestibility in East African ruminants. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 2008, 151, 185–190.
20. Sivakumar, A.V.N.; Singh, G.; Varshney, V.P. Antioxidants Supplementation on Acid Base Balance during Heat Stress in Goats. Asian-Australas. J. Anim. Sci. 2010, 23, 1462–1468.
21. O'Brien, M.D.; Rhoads, R.P.; Sanders, S.R.; Duff, G.C.; Baumgard, L.H. Metabolic adaptations to heat stress in growing cattle. Domest. Anim. Endocrinol. 2010, 38, 86–94.
22. Ma, X.; Jiang, Z.; Zheng, C.; Hu, Y.; Wang, L. Nutritional regulation for meat quality and nutrient metabolism of pigs exposed to high-temperature environment. J. Nutr. Food Sci. 2015, 5, 420.
23. Holinger, M.; Früh, B.; Stoll, P.; Pedan, V.; Kreuzer, M.; Bérard, J.; Hillmann, E. Long-Term Effects of Castration, Chronic Intermittent Social Stress, Provision of Grass Silage and Their Interactions on Performance and Meat and Adipose Tissue Properties in Growing-Finishing Pigs. Meat Sci. 2018, 145, 40–50.

24. St Pierre, N.R. Economic losses from heat stress by US livestock industries. J. Dairy Sci. 2003, 86, E52.

25. Baziz, H.A.; Geraert, P.A.; Padilha, J.C.F.; Guillaumin, S. Chronic heat exposure enhances fat deposition and modifies muscle and fat partition in broiler carcasses. Poult. Sci. 1996, 75, 505–513.

26. Mader, T.L.; Dahlquist, J.M.; Hahn, G.L.; Gaughan, J.B. Shade and wind barrier effects on summertime feedlot cattle p erformance. J. Anim. Sci. 1999, 77, 2065–2072.

27. Ponnampalam, E.N.; Burnett, V.F.; Norng, S.; Hopkins, D.L.; Plozza, T.; Jacobs, J.L. Muscle antioxidant (vitamin E) and major fatty acid groups, lipid oxidation and retail colour of meat from lambs fed a roughage-based diet with flaxseed or algae. Meat Sci. 2016, 111, 154–160.

28. England, E.M.; Scheffler, T.L.; Kasten, S.C.; Matarneh, S.K.; Gerrard, D.E. Exploring the unknowns involved in the tran sformation of muscle to meat. Meat Sci. 2013, 95, 837–843.

29. Cheah, K.S.; Cheah, A.M. Post-mortem changes in structure and function of ox muscle mitochondria. 1. Electron micro scopic and polarographic investigations. J. Bioenerg. 1971, 2, 85–92.

30. Tarrant, P.V. The Occurrence, Causes and Economic Consequences of Dark-Cutting in Beef—A Survey of Current Infor mation on the Problem of Dark-Cutting in Beef; Springer: Dordrecht, The Netherlands, 1981; pp. 3–36.

31. Liang, R.R.; Zhang, M.Y.; Zhang, M.H.; Luo, X. Effect of different acute heat stress degrees on amp-activated protein ki nase (ampk) in chicken meat. In Proceedings of the 64th International Congress of Meat Science Technology, Melbour ne, Australia, 12–17 August 2018.

32. Aksit, M.; Yalcin, S.; Ozkan, S.; Metin, K.; Ozdemir, D. Effects of temperature during rearing and crating on stress para meters and meat quality of broilers. Poult. Sci. 2006, 85, 1867–1874.

33. Xing, T.; Xu, X.L.; Zhou, G.H.; Wang, P.; Jiang, N.N. The effect of transportation of broilers during summer on the expre ssion of heat shock protein 70, postmortem metabolism, and meat quality. J. Anim. Sci. 2015, 93, 62–70.

34. Xing, T.; Xu, X.; Jiang, N.; Deng, S. Effect of transportation and preslaughter water shower spray with resting on AMP-a ctivated protein kinase, glycolysis, and meat quality of broilers during summer. Anim. Sci. J. 2016, 87, 299–307.

35. Wang, R.H.; Liang, R.R.; Lin, H.; Zhu, L.X.; Zhang, Y.M.; Mao, Y.W.; Dong, P.C.; Niu, L.B.; Zhang, M.H.; Luo, X. Effect of acute heat stress and slaughter processing on poultry meat quality and post-mortem carbohydrate metabolism. Poul t. Sci. 2017, 96, 738–746.

36. Downing, J.A.; Kerr, M.J.; Hopkins, D.L. The effects of pre-transport supplementation with electrolytes and betaine on p erformance, carcass yield, and meat quality of broilers in summer and winter. Livest. Sci. 2017, 205, 16–23.

37. Sandercock, D.A.; Hunter, R.R.; Nute, G.R.; Mitchell, M.A.; Hocking, P.M. Acute heat stress-induced alterations in bloo d acid-base status and skeletal muscle membrane integrity in broiler chickens at two ages: Implications for meat qualit y. Poult. Sci. 2001, 80, 418–425.

38. Wang, R.R.; Pan, X.J.; Peng, Z.Q. Effects of heat exposure on muscle oxidation and protein functionalities of pectoralis majors in broilers. Poult. Sci. 2009, 88, 1078–1084.

39. Van Laack, R.L.J.; Liu, C.-H.; Smith, M.O.; Loveday, H.D. Characteristics of pale, soft, exudative broiler breast meat. P oult. Sci. 2000, 79, 1057–1061.

40. Strasburg, G.M.; Chiang, W. Pale, soft, exudative Turkey—The role of ryanodine receptor variation in meat quality. Poul t. Sci. 2009, 88, 1497–1505.

41. Kadim, I.T.; Mahgoub, O.; Al-Marzooqi, W.; Al-Ajmi, D.S.; Al-Maqbali, R.S.; Al-Lawati, S.M. The influence of seasonal te mperatures on meat quality characteristics of hot-boned, m. psoas major and minor, from goats and sheep. Meat Sci. 2 008, 80, 210–215.

42. Apaoblaza, A.; Galaz, A.; Strobel, P.; Ramirez-Reveco, A.; Jerez-Timaure, N.; Gallo, C. Glycolytic potential, and activity of adenosine monophosphate kinase (AMPK), glycogen phosphorylase (GP) and glycogen debranching enzyme (GD E) in steer carcasses with normal (5.9) 24 h pH determined in M. longissimus dorsi. Meat Sci. 2015, 101, 83–89.

43. Tang, S.; Yu, J.M.; Zhang, M.; Bao, E.D. Effects of different heat stress periods on various blood and meat quality para meters in young arbor Acer broiler chickens. Can. J. Anim. Sci. 2012, 93, 453–460.

44. Gonzalez-Rivas, P.A.; Chauhan, S.S.; Ha, M.; Fegan, N.; Dunshea, F.R.; Warner, R.D. Effects of heat stress on animal physiology, metabolism, and meat quality: A review. Meat Sci. 2020, 162, 108025.

45. Kadim, I.T.; Mahgoub, O.; Khalaf, S. Effects of the transportation during hot season and electrical stimulation on meat q uality characteristics of goat Longissimus dorsi muscle. Small Rumin. Res. 2014, 121, 120–124.

46. Song, D.J.; King, A.J. Effects of heat stress on broiler meat quality. Worlds Poult. Sci. J. 2015, 71, 701–709.

47. Woelfel, R.L.; Owens, C.M.; Hirschler, E.M.; Martinez-Dawson, R.; Sams, A.R. The characterization and incidence of pale, soft, and exudative broiler meat in a commercial processing plant. Poult. Sci. 2002, 81, 579–584.

48. Zhang, X.; Owens, C.M.; Schilling, M.W. Meat: The edible flesh from mammals only or does it include poultry, fish, and seafood? Anim. Front. 2017, 7, 12–18.

49. Yost, J.; Kenney, P.; Slider, S.; Russell, R.; Killefer, J. Influence of selection for breast muscle mass on myosin isoform composition and metabolism of deep pectoralis muscles of male and female turkeys. Poult. Sci. 2002, 81, 911–917.

50. Wilhelm, A.E.; Maganhini, M.B.; Hernández-Blazquez, F.J.; Ida, E.I.; Shimokomaki, M. Protease activity and the ultrastructure of broiler chicken PSE (pale, soft, exudative) meat. Food Chem. 2010, 119, 1201–1204.

51. Liu, Z.; Liu, Y.; Xing, T.; Li, J.; Zhang, L.; Jiang, Y.; Gao, F. Transcriptome analysis reveals the mechanism of chronic heat stress on meat quality of broilers. J. Anim. Sci. Biotechnol. 2022, 13, 110.

52. Barbut, S.; Sosnicki, A.A.; Lonergan, S.M.; Knapp, T.; Ciobanu, D.C.; Gatcliffe, L.J.; Huff-Lonergan, E.; Wilson, E.W. Progress in reducing the pale, soft and exudative (PSE) problem in pork and poultry meat. Meat Sci. 2008, 79, 46–63.

53. Owens, C.M.; Alvarado, C.Z.; Sams, A.R. Research developments in pale, soft, and exudative turkey meat in North America. Poult. Sci. 2009, 88, 1513–1517.

54. Liu, Y.; Li, J.L.; Li, Y.J.; Gao, T.; Zhang, L.; Gao, F.; Zhou, G.H. Effects of dietary supplementation of guanidino acetic acid and combination of guanidino acetic acid and betaine on postmortem glycolysis and meat quality of finishing pigs. Anim. Feed. Sci. Tech. 2015, 205, 82–89.

55. Hughes, J.M.; Clarke, F.M.; Purslow, P.P.; Warner, R.D. Meat color is determined not only by chromatic heme pigments but also by the physical structure and achromatic light scattering properties of the muscle. Compr. Rev. Food Sci. Food Saf. 2019, 19, 44–63.

56. Zhang, M.; Dunshea, F.R.; Warner, R.D.; DiGiacomo, K.; Amponsah, R.O.; Chauchan, S.S. Impacts of heat stress on meat quality and strategies for amelioration: A review. Int. J. Biometeorol. 2020, 64, 1613–1628.

57. IPCC. Special Report: Global Warming of 1.5 °C; IPCC: Incheon, Republic of Korea, 2018; Available online: https://www.ipcc.ch/sr15/ (accessed on 5 February 2023).

58. Dettleff, P.; Zuloaga, R.; Fuentes, M.; Gonzalez, P.; Aedo, J.; Estrada, J.M.; Molina, A.; Valdés, J.A. Physiological and molecular responses to thermal stress in red cusk-eel (Genypterus chilensis) juveniles reveals atrophy and oxidative damage in skeletal muscle. J. Therm. Biol. 2020, 94, 102750.

59. Xu, Y.; Lai, X.; Li, Z.; Zhang, X.; Luo, Q. Effect of chronic heat stress on some physiological and immunological parameters in different breeds of broilers. Poult. Sci. 2018, 97, 4073–4082.

60. Sula, M.J.; Winslow, C.M.; Boileau, M.J.; Barker, L.D.; Panciera, R.J. Heat-related injury in lambs. J. Vet. Diagn. Investig. 2012, 24, 772–776.

61. Freitas, A.S.; Carvalho, L.M.; Soares, A.L.; Oliveira, M.D.S.; Madruga, M.S.; Neto, A.D.S.; Carvalho, R.H.; Ida, E.I.; Shimokomaki, M. Pale, Soft and Exudative (PSE) and Dark, Firm and Dry (DFD) Meat Determination in Broiler Chicken Raised Under Tropical Climate Management Conditions. Int. J. Poult. Sci. 2017, 16, 81–87.

62. Adzitey, F.; Nurul, H. Pale soft exudative (PSE) and dark firm dry (DFD) meats: Causes and measures to reduce these incidences. Int. Food Res. J. 2011, 18, 11–20.

63. Kim, Y.H.B.; Warner, R.D.; Rosenvold, K. Influence of high pre-rigor temperature and fast pH fall on muscle proteins and meat quality: A review. Anim. Prod. Sci. 2014, 54, 375–395.

64. Warner, R.D.; Dunshea, F.R.; Gutzke, D.; Lau, J.; Kearney, G. Factors influencing the incidence of high rigor temperature in beef carcasses in Australia. Anim. Prod. Sci. 2014, 54, 363–374.

65. Gregory, N.G. How climatic changes could affect meat quality. Food Res. Int. 2010, 7, 1866–1873.

66. D'Souza, D.N.; Leury, B.J.; Dunshea, F.R.; Warner, R.D. Effect of on-farm and pre-slaughter handling of pigs on meat quality. Aust. J. Agric. Res. 1998, 49, 1021–1025.

67. Minton, J.E. Function of the hypothalamic-pituitary-adrenal axis and the sympathetic nervous system in models of acute stress in domestic farm animals. J. Anim. Sci. 1994, 72, 1891–1898.

68. Afsal, A.; Sejian, V.; Madiajagan, B.; Krishnan, G. Heat Stress and Livestock Adaptation: Neuro-endocrine Regulation. Int. J. Vet. Anim. Med. 2018, 1, 1–8.

69. Kadim, I.T.; Mahgoub, O.; Al-Kindi, A.; Al-Marzooqi, W.; Al-Saqri, N.M. Effects of transportation at high ambient temperatures on physiological responses, carcass, and meat quality characteristics of three breeds of Omani goats. Meat Sci. 2006, 73, 626–634.

70. Kuo, T.; Harris, C.A.; Wang, J.-C. Metabolic functions of glucocorticoid receptor in skeletal muscle. Mol. Cell. Endocrinol. 2013, 380, 79–88.

71. Schiaffino, S.; Dyar, K.A.; Ciciliot, S.; Blaauw, B.; Sandri, M. Mechanisms regulating skeletal muscle growth and atrophy. FEBS J. 2013, 280, 4294–4314.

72. Bell, R.A.V.; Al-Khalaf, M.; Megeney, L.A. The beneficial role of proteolysis in skeletal muscle growth and stress adaptation. Skelet. Muscle 2016, 6, 16.

73. Braun, T.P.; Marks, D.L. The regulation of muscle mass by endogenous glucocorticoids. Front. Physiol. 2015, 6, 12.

74. Sapolsky, R.M.; Romero, L.M.; Munck, A.U. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. Endocr. Rev. 2000, 21, 55–89.

75. Scanes, C.G. Biology of stress in poultry with emphasis on glucocorticoids and the heterophil to lymphocyte ratio. Poult. Sci. 2016, 95, 2208–2215.

76. Lu, Q.; Wen, J.; Zhang, H. Effect of chronic heat exposure on fat deposition and meat quality in two genetic types of chicken. Poult. Sci. 2007, 86, 1059–1064.

77. Cai, Y.; Song, Z.; Zhang, X.; Wang, X.; Jiao, H.; Lin, H. Increased de novo lipogenesis in liver contributes to the augmented fat deposition in dexamethasone-exposed broiler chickens (Gallus gallus domesticus). Comp. Biochem. Physiol. C Toxicol. Pharmacol. 2009, 150, 164–169.

78. Wang, X.J.; Song, Z.G.; Jiao, H.C.; Lin, H. Skeletal muscle fatty acids shift from oxidation to storage upon dexamethasone treatment in chickens. Gen. Comp. Endocrinol. 2012, 179, 319–330.

79. Wang, X.J.; Wei, D.L.; Song, Z.G.; Jiao, H.C.; Lin, H. Effects of fatty acid treatments on the dexamethasone-induced intramuscular lipid accumulation in chickens. PLoS ONE 2012, 7, e36663.

80. Cruzen, S.M.; Boddicker, R.L.; Graves, K.L.; Johnson, T.P.; Arkfeld, E.K.; Baumgard, L.H.; Ross, J.W.; Safranski, T.J.; Lucy, M.C.; Lonergan, S.M. Carcass composition of market weight pigs subjected to heat stress in utero and during finishing. J. Anim. Sci. 2015, 93, 2587–2596.

81. Qu, H.; Yan, H.; Lu, H.; Donkin, S.S.; Ajuwon, K.M. Heat stress in pigs is accompanied by adipose tissue–specific responses that favor increased triglyceride storage. J. Anim. Sci. 2016, 94, 1884–1896.

82. Carra, S.; Alberti, S.; Arrigo, P.A.; Benesch, J.L.; Benjamin, I.J.; Boelens, W.; Bartelt-Kirbach, B.; Brundel, B.J.; Buchner, J.; Bukau, B.; et al. The growing world of small heat shock proteins: From structure to functions. Cell Stress Chaperones 2017, 22, 601–611.

83. Newcom, D.W.; Stadler, K.J.; Baas, T.J.; Goodwin, R.N.; Parrish, F.C.; Wiegand, B.R. Breed differences and genetic parameters of myoglobin concentration in porcine longissimus muscle. J. Anim. Sci. 2004, 82, 2264–2268.

84. Prasad, A.S.; Bao, B. Review, Molecular Mechanisms of Zinc as a Pro-Antioxidant Mediator: Clinical Therapeutic Implications. Antioxidants 2019, 8, 164.