Meta-analysis to predict the effects of temperature stress on meat quality of poultry

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ABSTRACT Temperature stress (**TS**) is a significant issue in poultry production, which has implications for animal health and welfare, productivity, and industry profitability. Temperature stress, including both hot (heat stress) and cold conditions (cold stress), is associated with increased incidence of meat quality defects such as pale, soft, and exudative (**PSE**) and dark, firm, and dry (**DFD**) meat costing poultry industries millions of dollars annually. A meta-analysis was conducted to determine the effect of ambient TS on meat quality parameters of poultry. Forty-eight publications which met specific criteria for inclusion were identified through a systematic literature review. Temperature stress was defined by extracting 2 descriptors for each treatment mean from the chosen studies: (1) temperature imposed for the experimental treatments (°C) and duration of temperature exposure. Treatment duration was categorized for analysis into acute (≤24 h) or chronic (>24 h) treatments. Meat quality parameters considered were color (L*-a*-b* scheme), pH (initial and ultimate), drip loss, cooking loss, and shear force. Linear mixed model analysis, including study as a random effect, was used to determine the effect of treatment temperature and duration on meat quality. Model evaluation was conducted by performing a k-fold cross-validation to estimate test error, and via assessment of the root mean square prediction error (**RMSPE**), and concordance correlation coefficient (**CCC**). Across both acute and chronic durations, treatment temperature was found to have a significant effect on all studied meat quality parameters. As treatment temperature increased, meat demonstrated characteristics of PSE meat and, as temperature decreased, meat demonstrated characteristics of DFD meat. The interaction between treatment temperature and duration was significant for most traits, however, the relative impact of treatment duration on the studied traits was inconsistent. Acute TS had a larger effect than chronic TS on ultimate pH, and chronic stress had a more considerable impact on color traits (L* and a*). This meta-analysis quantifies the effect of ambient TS on poultry meat quality. However, quantitative effects were generally small, and therefore may or may not be of practical significance from a processing perspective.

Key words: color, cooking loss, drip loss, pH, shear force

INTRODUCTION

When ambient temperature deviates from an animal's thermoneutral zone, it forces the animal to employ additional heat-saving or heat-dissipating measures (Silva, 2006). Exposure to temperature stress (**TS**) is an important issue in poultry production since poultry are inefficient at regulating body temperature. In particular, poultry are at high risk in hot environments because they do not possess functional sweat glands, have a high core body temperature, and a rapid metabolism (Jahejo et al., 2016). However, both heat and cold can negatively impact poultry growth and production performance (Zhang et al., 2011; Lara and Rostagno, 2013; Zhao et al., 2013; Habibian et al., 2014; Tawfeek et al., 2014).

Heat and cold stress have also been implicated in the development of meat quality defects in poultry, such as pale, soft, and exudative (**PSE**), and dark, firm, and dry (**DFD**) meat (Barbut et al., 2005). In susceptible birds, heat stress can accelerate the postmortem (**PM**) degradation of muscle glycogen to lactic acid, which causes muscle pH to decrease rapidly after slaughter

(Owens et al., 2009; Barbut, 2015). This rapid drop in pH, combined with the warm muscle, denatures the muscle proteins, causing the meat to have a low water holding capacity, pale color, and exude moisture (Pietrzak et al., 1997; King and Whyte, 2006; Carvalho et al., 2014). The rise in consumer demand for deboned smaller cuts and further processed products has increased focus on the presentation of skinless portions. This means meat color and water-holding capacity (**WHC**), which are highly related to consumer acceptance, are more important (Min and Ahn, 2012; Barbut, 2015). As such, PSE meat has been estimated to cost both the US turkey and broiler industry $200 million annually (Lubritz, 2007; Owens et al., 2009).

While heat stress is more likely to cause PSE meat, cold stress is implicated more often in DFD meat development. Several studies have found correlations between cold exposure during rearing and transportation and the incidence of DFD meat in poultry (Froning et al., 1978; Babji et al., 1982; Holm and Fletcher, 1997; Bianchi et al., 2006). The increased metabolic demand to maintain core body temperature during cold conditions results in the use of muscle glycogen as an energy source (Lee et al., 1976; Haman et al., 2002,2005; Dadgar et al., 2011, 2012a). The depletion of muscle glycogen, prior to slaughter, decreases the PM potential lactate formation in the meat and results in higher pH of the muscle (Berri et al., 2005; Dadgar et al., 2011). Eventually, this results in a darker product that is unappealing from a consumer perspective and as such, can result in economic loss to the industry.

Poultry production is year-round, occurring during many types of inclement weather, so TS can be a concern during all phases of production. Typically, studies use chronic exposure (>24 h) to simulate the long-term or seasonal effects of TS during production, whereas acute exposure (<24 h) is typically used to simulate short-term or daily fluctuations in ambient temperature soon before slaughter (i.e., during transit). Both chronic and acute TS affect poultry meat quality parameters; however, acute stress, as opposed to chronic, is typically implicated in the development of PSE meat since the exposure to extreme temperatures soon before slaughter has a more substantial effect on meat quality (Barbut et al., 2008; Gonzalez-Rivas et al., 2020). However, this effect may be related to genetic susceptibility in certain birds, meaning that not all animals are prone to the malignant hyperthermia associated with heat stress-induced PSE meat (Barbut, 2015). Interestingly, studies of swine and ruminants report that chronic stress can lead to the development of DFD meat in these species (Gregory, 2010; Adzitey and Nurul, 2011). In poultry, the relationship between acute and chronic exposure is not clear. Studies of TS in poultry use widely different stress durations leading to a substantial source of variation in the results. Few studies include both short-term and long-term stress durations within the same experiment, so it is difficult to elucidate which treatment has a larger effect on meat quality.

There have been several reviews detailing the effect of TS on meat quality in poultry, ruminants, and swine (Ali et al., 2008; Xing et al., 2019; Gonzalez-Rivas et al., 2020) as well as describing meat quality defects in poultry (Lesiow and Kijowski, 2003; Barbut, 2009; Owens et al., 2009; Petracci et al., 2009; Mir et al., 2017). However, to our knowledge, a quantitative meta-analysis focusing on the effect of TS on poultry meat quality has not yet been conducted. Meta-analyses are useful for accounting for variability between studies and can overcome the limitations of small sample sizes in individual studies. Meta-analysis can also overcome the subjective nature of qualitative reviews and help interpret conflicting results in the literature.

The objective of the present study was therefore to synthesize the results of the numerous empirical studies in this area and quantify the effect of TS on various parameters of poultry meat quality. An additional objective was to investigate whether the studied meat quality traits are affected differently by acute and chronic exposure to TS.

MATERIALS AND METHODS

Dataset Development

A systematic literature search was conducted in February 2020 using the Web of Science database and hand-searching the Poultry Science journal. No temporal or language restrictions were applied to the searches. Keyword combinations were used to identify papers that included poultry, stress, and meat quality which formed the initial dataset for this study (N = 1389 studies). Exclusion criteria were then applied to this dataset to determine the studies that will be included in the meta-analysis (Figure 1).

Papers were excluded from further analysis if they did not include poultry, stress, or meat quality in the title, abstract, or keywords or were not primary research articles (i.e., reviews or conference abstracts). Poultry species considered for this meta-analysis were broiler chickens and turkeys.

Full-length papers were reviewed to determine if they included the effect of TS (i.e., heat and cold stress) on typical meat quality parameters. All studies included in the analysis were required to have TS as an experimental treatment. This means that the objective of the studies included needed to focus on the impact of temperature stress on meat quality outcomes, and comparable to a control (nonstress conditions). Meat quality parameters of interest included color traits of lightness (L*), redness (a*), yellowness (b*), pH traits (initial, ultimate), drip loss (%), cooking loss (%), and shear force (N). Color was recorded in all selected studies based on the Commission Internationale de l'Eclairage dimensions (CIE, 1976). Meat color was recorded between 0.25 and 48 h PM in the final database, with the mean recording time of 24 h PM. Initial pH was defined as the first pH measurement taken after slaughter. In the final database, initial pH measurements were taken from 0 to
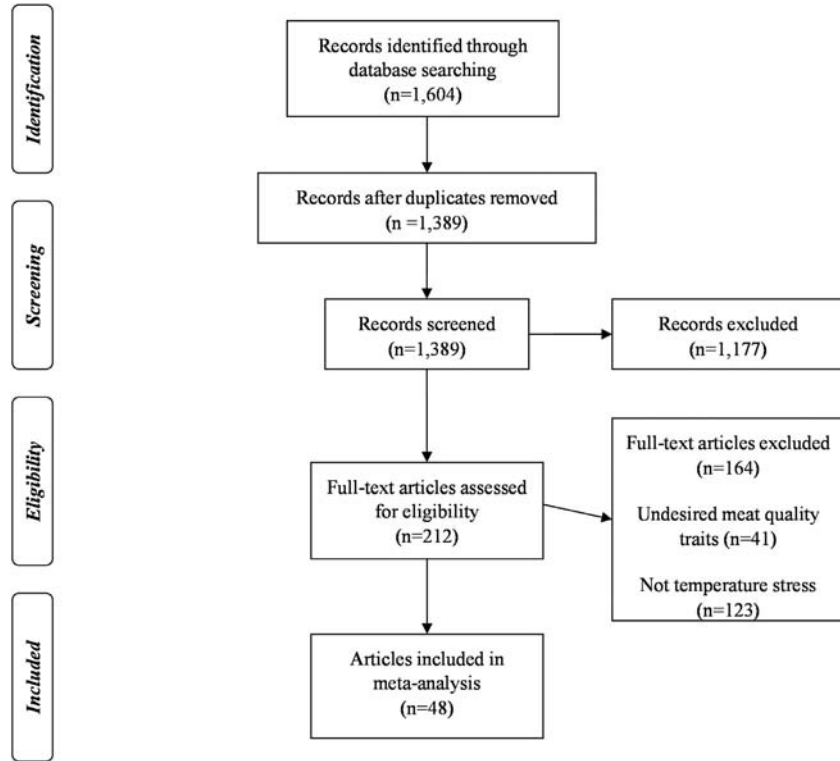
Figure 1. Literature funnel (Preferred reporting items for systematic reviews and meta-analyses (PRISMA) diagram adapted from (Moher et al., 2009).

240 min PM. The average measurement time was approximately 45 min PM. Ultimate pH was defined as the pH measurement recorded at 24 h PM. Of the initial 1,389 search results, 48 studies met the criteria for inclusion in the meta-analysis and are summarized in Table 1.

Additional parameters extracted included species (broiler or turkey), experimental treatment temperature, experimental treatment duration, slaughter age, and muscle (breast vs. thigh). Typically, each study has multiple experimental treatments (e.g., a control treatment and a heat stress treatment) which were extracted separately from the study with the corresponding treatment means for the meat quality traits. Each treatment represented a separate row of data in the developed database. To collapse variation in study design for analysis, the duration of TS was categorized for each treatment mean as either control (no TS applied), acute (≤24 h) or chronic (>24 h). Treatment means for cyclic TS (stress applied for <24 h for more than 2 consecutive days) were reclassified as chronic stress.

Descriptive statistics (mean, median, min, max, and standard deviation) for the dependent and independent variables in the final database (before model development) are shown in Table 2.

Model Development

Prior to full model development, a correlation analysis was performed on the dependent variables using PROC CORR in SAS to identify key potential drivers of meat quality outcomes, as well as redundant and collinear variables within the database (Table 3). Due to the high number of variable correlations, $r > 0.4$ was used as an arbitrary cut-off value for discussion. All correlations, regardless of correlation coefficient, are reported in Table 3.

To model the effect of TS on meat quality, a linear mixed model analysis was performed with study modeled as a random effect (St-Pierre, 2001) and treatment temperature as the main fixed effect. The general model used was:

$$Y_{ij} = X_i a_i + b_i + X a_i b_i + m + \varepsilon_{ijk} \qquad (1)$$

where $i = 1, \ldots, 48$ studies, $j = 1, \ldots, n_i$ treatment means, X_i = treatment temperature in Celcius, a_i = slope term for temperature, b_i =treatment duration (control, acute, or chronic), $a_i b_i$ = interaction between temperature and duration, m = additional variables examined (species, slaughter age, muscle type, measurements time), and ε_{ijk} = residual error of the model. The fixed effect component of the model was expanded as additional variables were considered. The Y variables considered for analysis were L*, a*, b*, initial pH, ultimate pH, drip loss, cooking loss, and shear force.

Models were developed and tested using PROC MIXED in SAS (SAS version 9.4, SAS/STAT, SAS Institute Inc, Cary, NC). Fixed effects were tested against a P-value of 0.05 for inclusion in the model. A backward stepping modeling approach was taken by first creating a 'full' model (Equation 1), with temperature, species, slaughter age, muscle type, measurement time, and stress duration as x-variables (depending on the trait), and then sequentially removing the least

Table 1. Summary of studies used to assess the effect of TS on meat quality of poultry.

Reference	Country	Species	Temp. type[1]	Stress type[2]	Control temperature[3]	Treatment temperature[3]
Aksit et al. (2006)	Turkey	broiler	CON, HS	Chronic*	22	31
Babji et al. (1982)	USA	turkey	CON, HS, CS	Acute	21	5 & 38
Bautista et al. (2016)	Mexico	broiler	CON, HS	Acute	24	40
Bianchi et al. (2006)	Italy	broiler	CON, HS, CS	Acute	15	12 & 18
Brossi et al. (2018)	Brazil	broiler	CON, HS	Acute	22	35
Cheng et al. (2018)	China	broiler	CON, HS	Chronic	20	32.5
Chiang et al. (2008)	USA	turkey	CON, HS	Chronic	23	35
Cramer et al. (2018)	USA	broiler	CON, HS	Chronic	22	32
Dadgar et al. (2011)	Canada	broiler	CON, CS	Acute	21	-8.5
Dadgar et al. (2012b)	Canada	broiler	CON, CS	Acute	22	-8.25
Dai et al. (2009)	China	broiler	CON, HS	Chronic	23	28
Debut et al. (2003)	France	broiler	CON, HS	Acute	21	35
Feng et al. (2008)	China	broiler	CON, HS	Chronic	22	31
Fernandes et al. (2016)	Brazil	broiler	HS	Acute	NA	33
Ferreira et al. (2015)	Brazil	broiler	CON, HS, CS	Chronic	27.5	23 & 32
Froning et al. (1978)	USA	turkey	HS, CS	Acute	NA	4 & 42
Goo et al. (2019)	South Korea	broiler	CON, HS	Chronic	20	27.8
Gu et al. (2008)	China	broiler	CON, HS, CS	Chronic	22	15 & 33
Hadad et al. (2014)	Israel	broiler	CON, HS	Chronic	26	32
Hashizawa et al. (2013)	Japan	broiler	CON, HS	Chronic	24	30
Henrikson et al. (2018)	Canada	turkey	CON, CS	Acute	20	-18
Holm and Fletcher (1997)	Sweden	broiler	CON, HS, CS	Acute	18	7 & 29
Kanani et al. (2017)	Iran	broiler	CON, HS	Chronic	22	32
Liu et al. (2019)	China	broiler	CON, HS	Chronic	26	32
Lu et al. (2007)	China	broiler	CON, HS	Chronic	21	34
Lu et al. (2017)	China	broiler	CON, HS	Chronic	22	32
Mazur-Kuśnirek et al. (2019)	Poland	broiler	CON, HS	Chronic	20.5	34
N'dri et al. (2007)	France	broiler	CON, HS	Chronic	20	30
Owens et al. (2000b)	USA	turkey	CON, HS	Chronic	17	34
Petracci et al. (2001)	Italy	broiler	CON, HS, CS	Acute	29.5	24 & 34
Sandercock et al. (2001)	UK	broiler	CON, HS	Acute	21	32
Schneider et al. (2012)	Canada	broiler	CON, HS, CS	Acute	21	7 & 30
Shao et al. (2019)	China	broiler	CON, HS	Chronic	23	35
Sifa et al. (2018)	China	broiler	CON, HS	Acute	23	34
Skomorucha et al. (2010)	Poland	broiler	CON, HS	Chronic	21	35
Tang et al. (2013)	China	broiler	CON, HS	Acute	22	37
Tavaniello et al. (2020)	Italy	broiler	HS	Chronic	NA	30
Toplu et al. (2014)	Turkey	broiler	CON, HS	Chronic*	24	35
Vermette et al. (2017)	Canada	turkey	CON, HS	Acute	20	35
Wan et al. (2018)	China	broiler	CON, HS	Chronic	22	34
Wang et al. (2017)	China	broiler	CON, HS	Acute	25	36
Wen et al. (2019)	China	broiler	CON, HS	Chronic	22	34
Zahoor et al. (2016)	Pakistan	broiler	CON, CS	Chronic	21	17
Zeferino et al. (2016)	Brazil	broiler	CON, HS	Chronic	24	32
Zhang et al. (2012)	China	broiler	CON, HS	Chronic*	23	35
Zhang et al. (2017)	China	broiler	CON, HS	Chronic	22	33
Zhang et al. (2019)	China	broiler	CON, HS	Acute	25	38
Zhao et al. (2019)	China	broiler	CON, HS	Chronic	22	34

[1]CON, control treatment; CS, cold stress treatment; HS, heat stress treatment.
[2]Acute = stress treatments applied for ≤24 h, Chronic = stress treatments applied for >24 h.
[3]Average control or treatment temp. in°C, NA = control temp. not specified.
*Study contains cyclic stress treatments which have been reclassified as chronic.

significant term at each step and evaluating the change in the significance in the remaining variables. At each step, the residuals were assessed for normality, and the Akiake Information Criterion (**AICc**)

Table 2. Descriptive statistics for X variables and meat quality traits included in the meta-analysis.

Variable	Mean	SD	Min	Max	Median	N
Lightness (L*)	51.19	5.947	36.600	71.100	51.270	195
Yellowness (b*)	7.02	5.029	−3.800	18.480	6.320	167
Redness (a*)	6.82	5.499	0.002	27.400	4.800	169
Initial pH	6.18	0.284	5.570	6.840	6.170	129
Ultimate pH	6.28	4.292	5.300	7.070	5.920	161
Cooking loss (%)	21.78	9.657	3.700	49.400	49.400	108
Drip loss (%)	1.96	1.442	0.320	5.720	1.560	77
Shear force (N)	31.12	16.551	11.470	77.960	27.670	90

value was evaluated for model improvement/worsening. Since color and pH measurements were not always taken at the same time PM in the different studies, the 'measurement time' variable was included in the analysis for these traits to account for some of the resulting variation.

To account for the heterogeneity in sample size and error between treatment means across experiments, the WEIGHT statement in PROC MIXED was used to weight the observations by the inverse of their variance. To do so, the inverse of the squared standard error of the mean (**SEM**) of each observation was determined. This value was then divided by the average squared SEM inverse of all observations, which centers the value around 1, and is the metric used to weight observations (St-Pierre, 2001).

Table 3. Pearson correlation coefficients between meat quality outcome variables in the database.

Trait	L*	a*	b*	pH initial	pH ultimate	Drip loss	Cooking loss	Shear force	Temperature[3]	Age[4]
Lightness (L*)	1									
Redness (a*)	-0.210[1]	1								
Yellowness (b*)	0.254[1]	0.0297	1							
Initial pH	0.0288	-0.0271	-0.325[1]	1						
Ultimate pH	-0.482[2]	0.0264	-0.201[1]	0.292[1]	1					
Drip loss (%)	0.452[1]	-0.111	0.292[1]	0.173	-0.439[1]	1				
Cooking loss (%)	0.241[1]	-0.285[1]	-0.105	-0.559[2]	-0.397[2]	0.606[2]	1			
Shear force (N)	-0.107	-0.0343	-0.0343	0.0330	-0.0824	0.440[1]	0.299[1]	1		
Temperature	0.385[2]	0.0589	0.459[2]	-0.341[2]	-0.494[2]	0.415[1]	0.441[2]	0.159	1	
Age	0.123	0.154	-0.275[1]	-0.276[1]	-0.202[1]	-0.286[1]	0.241[1]	0.484[2]	0.0842	1

[1] $P < 0.05$.
[2] $P < 0.0001$.
[3] Average treatment temperature (°C).
[4] Age in days when birds were slaughtered.

To identify individual observations with a significant influence on the parameter estimates (outliers), the Cook's distance statistic was computed for each observation for each of the trait models in PROC MIXED. Cook's distance represents the change in fitted response values of the regression after the removal of an observation (Cook, 1977). Influential observations with a Cook's distance $>4/n$, where n represents the total number of treatment mean observations, were removed from the data set in a step-wise sequential manner.

Model Evaluation

After the final models were developed, a k-fold cross-validation approach was taken to determine the best model for each meat quality trait based on the calculated test error. The developmental dataset was divided into 5 folds, and each model was refitted on 4 of the 5 folds in turn, keeping one fold for evaluation. Test error (**CV$_K$**, Equation 2), root mean square prediction error (the root of the MSPE, Equation 3), and concordance correlation coefficient (**CCC**, Equations 7) were then calculated for the refitted model on each of the remaining folds (not used for model development), and can be summarized as:

$$CV_K = \sum_{k=1}^{K} \frac{n_K}{n} MSE_K \tag{2}$$

where K represents each fold (1-5), n_K = number of observations in the kth fold, n = the total number of observations, and MSE_K = mean squared error of the kth fold.

$$MSPE = \frac{\sum_{i=1}^{n} (Y_{Pred} - Y_{Obs})^2}{n} \tag{3}$$

Where n = total number of treatment mean observations, Y_{Pred} = predicted value, and Y_{Obs} = observed value. Root mean square prediction error (**RMSPE**) was calculated by taking the square root of the MSPE and is expressed as a percentage of the observed mean. RMSPE provides an estimate of the overall prediction error for the equation.

The RMSPE was decomposed into error due to bias (**ECT**, Equation 4), error due to deviation of the regression slope from unity (**ER**, Equation 5), and error due to random disturbance (**ED**, Equation 6) (Bibby and Toutenburg, 1977).

$$ECT = \left(\overline{O} - \overline{P}\right)^2 \tag{4}$$

$$ER = (S_P - R \times S_O)^2 \tag{5}$$

$$ED = \left(1 - R^2\right) \times (S_O)^2 \tag{6}$$

Where $\overline{O}$ = observed mean, $\overline{P}$ = predicted mean, S_O and S_P = observed and predicted standard deviations, and R = Pearson correlation coefficient.

The CCC, or reproducibility index, simultaneously assess a model's precision and accuracy (Lin, 1989; Tedeschi, 2006). The CCC ranges from -1 to 1, with -1 indicating that the observed and predicted values are perfectly unrelated, 0 indicating no relationship, and 1 indicating they are perfectly related (Lin, 1989). The CCC was calculated as:

$$CCC = R \times C_b \tag{7}$$

where R is the Pearson correlation coefficient which indicates the equation's precision, and C_b is a bias correction factor which indicates the equation's accuracy (Equation 8). C_b ranges from 0 to 1 where 1 indicates there is no deviation of the regression line from the line of unity (Tedeschi, 2006). C_b is calculated as:

$$C_b = \frac{2}{[v + 1/v + \mu^2]'} \tag{8}$$

where:

$$v = \frac{S_O}{S_P} \tag{9}$$

$$\mu = \frac{\overline{O} - \overline{P}}{(S_O \times S_P)^{-1/2'}} \tag{10}$$

and where v is an indicator of change in standard deviation, or scale shift, between predicted and observed

values. The parameter μ is an indicator of location shift whereby a positive μ value indicates equation under-prediction and a negative μ value indicates over-prediction.

The model which yielded the lowest test error (CV_K) for each trait was chosen as the best developed model. Models reported are then those developed on the full dataset. The MSPE and CCC represent the average ± SEM values across the 5 k-folds.

To test for slope and mean bias, an analysis of the residuals was performed using PROC REG. The conditional residuals were regressed on the predicted values to obtain slope/intercept parameter estimates which were tested for significance against zero. A visual assessment of predicted values vs. observed and predicted values vs. residuals was also performed for color traits, pH traits, and cooking loss, drip loss, and shear force traits using PROC SGPLOT.

Subanalysis: Heat vs. Cold Stress

For the general equations, heat and cold stress studies were grouped together, however, a subanalysis was also conducted to compare the effect of heat stress versus cold stress on meat quality attributes in poultry. This attribute of the TS variable was not included in the main model development section due to the imbalanced nature of the database with respect to the number of heat stress (N = 131) and cold stress (N = 36) treatment means. Within the subanalysis, treatment means from each study were classified as either control (standard commercial temperature, no TS applied), heat stress, or cold stress. Stress type was included as a categorical fixed effect in the best prediction model for each meat quality trait in place of the temperature variable. Other significant fixed effects included in the best prediction model for each trait (i.e., muscle type or slaughter age) were kept in the model. Models were run in PROC MIXED of SAS to derive least-squared means for the heat stress and cold stress treatments for each meat quality trait. P-values from pairwise comparisons were adjusted using the Tukey HSD method to account for the effect of multiple comparisons.

RESULTS

Preliminary analysis in PROC CORR of the continuous X and Y variables are presented in Table 3. For the color traits, correlations where R > 0.4 included the correlation between L* and ultimate pH (R = −0.482, $P <$ 0.0001), and L* and drip loss (R = 0.452, $P <$ 0.05). For the pH traits, correlations where R > 0.4 included the correlation between initial pH and cooking loss (R = −0.559, $P <$ 0.0001), as well as between ultimate pH and drip loss (R = −0.439, $P <$ 0.05). For drip loss, cooking loss, and shear force traits, correlations where R > 0.4 included drip loss and cooking loss (R = 0.606, $P <$ 0.0001), as well as drip loss and shear force (R = 0.440, $P <$ 0.05). Temperature was significantly correlated with all studied traits, except for a* and shear force ($P <$ 0.05). Slaughter age was significantly correlated with b*, initial pH, ultimate pH, drip loss, cooking loss, and shear force ($P <$ 0.05).

Models developed using the mixed model approach are presented in Tables 4−6, and model evaluation statistics in Table 7. In Tables 4−6, one model may be documented across multiple rows if it contained categorical x continuous variable interactions (e.g., a separate equation was developed for turkeys vs. broilers, TS type, or muscle type).

Color Traits (L*, a*, b*)

Lightness (L*) The best prediction model included the fixed effects of slaughter age within species ($P <$ 0.0001), the interaction between stress duration (control vs. acute vs. chronic) and temperature ($P <$ 0.0001), as well as PM measurement time ($P <$ 0.05) (Model 1, Tables 4 and 7). Model evaluation (Table 7) shows a low RMSPE (2.47%) with the majority of error coming from random sources (ED, 93.4%), a high CCC (0.92), and a CV_k of 1.9%, indicating good overall fit of the data and

Table 4. Estimated parameters of linear mixed models for meat lightness (L*), redness (a*), and yellowness (b*) obtained for broilers or turkeys undergoing TS.[1]

Trait	Model[2]	Equation	Species	Muscle	Intercept	Stress[3]	Temperature[4]	Species × Age[5]	Time[6]
L*	1	L1	Broiler	-	56.19 ± 2.703	Control	0.03 ± 0.015	−0.16 ± 0.065	0.06 ± 0.026
L*	1	L2	Broiler	-	56.19 ± 2.703	Acute	0.02 ± 0.015	−0.16 ± 0.065	0.06 ± 0.026
L*	1	L3	Broiler	-	56.19 ± 2.703	Chronic	0.07 ± 0.021	−0.16 ± 0.065	0.06 ± 0.026
L*	1	L4	Turkey	-	56.19 ± 2.703	Control	0.03 ± 0.015	−0.07 ± 0.013	0.06 ± 0.026
L*	1	L5	Turkey	-	56.19 ± 2.703	Acute	0.02 ± 0.015	−0.07 ± 0.013	0.06 ± 0.026
L*	1	L6	Turkey	-	56.19 ± 2.703	Chronic	0.07 ± 0.021	−0.07 ± 0.013	0.06 ± 0.026
a*	2	R1	-	Breast	5.27 ± 0.405	-	-0.02 ± 0.007	-	-
a*	2	R2	-	Thigh	7.06 ± 0.606	-	-0.02 ± 0.007	-	-
b*	3	Y1	-	-	7.06 ± 0.821	-	0.02 ± 0.010	-	-

[1]Empty boxes, denoted with (-), indicate that the effect is not included in the best prediction model. Parameter estimates for temperature represent the interaction between stress and temperature when stress type is specified. If stress type is not specified (-), then the interaction was not included in the best prediction model.

[2]Equations with the same model ID were parameterized within the same statistical model.

[3]Control = no treatment applied, Acute = TS for ≤24 h, Chronic = TS for >24 h.

[4]Average treatment temperature (°C).

[5]Interaction between Species and Age in days when birds were slaughtered.

[6]Time in hour PM that the color measurement was taken.

Table 5. Estimated parameters of linear mixed models for meat initial pH (pH$_i$) and ultimate pH (pH$_u$) obtained for broilers or turkeys undergoing TS.[1]

Trait	Model[2]	Equation	Species	Muscle	Intercept	Stress[3]	Temperature[4]	Species × age[5]	Time[6]
pH$_i$	4	PI1	Broiler	-	6.939 ± 0.1822	-	−0.002 ± 0.0011	−0.013 ± 0.0043	−0.002 ± 0.0001
pH$_i$	4	PI2	Turkey	-	6.939 ± 0.1822	-	−0.002 ± 0.0011	−0.005 ± 0.0014	−0.002 ± 0.0001
pH$_u$	5	PU1	-	Breast	5.906 ± 0.0091	-	−0.002 ± 0.0004	-	-
pH$_u$	5	PU2	-	Thigh	6.119 ± 0.0304	-	−0.002 ± 0.0004	-	-

[1]Empty boxes, denoted with (-), indicate that the effect is not included in the best prediction model. Parameter estimates for temperature represent the interaction between stress and temperature when stress type is specified. If stress type is not specified (-), then the interaction was not included in the best prediction model.
[2]Equations with the same model ID were parameterized within the same statistical model.
[3]Control = no treatment applied, Acute = TS for ≤24 h, Chronic=TS for >24 h.
[4]Average treatment temperature (°C).
[5]Interaction between Species and Age in days when birds were slaughtered.
[6]Time in minute PM that the pH measurement was taken.

Table 6. Estimated parameters of linear mixed models for meat drip loss (%), cooking loss (%), and shear force (N) for broilers or turkeys undergoing TS.[1]

Trait	Model[2]	Equation	Species	Muscle	Intercept	Stress[3]	Temperature[4]	Species × age[5]	Time[6]
Drip loss	6	D1	-	-	2.129 ± 0.2715	Control	0.003 ± 0.0027	-	-
Drip loss	6	D2	-	-	2.129 ± 0.2715	Acute	0.004 ± 0.0022	-	-
Drip loss	6	D3	-	-	2.129 ± 0.2715	Chronic	0.010 ± 0.0022	-	-
Cooking loss	7	C1	-	Breast	21.664 ± 1.3298	-	0.045 ± 0.0176	-	-
Cooking loss	7	C2	-	Thigh	24.831 ± 1.7958	-	0.045 ± 0.0176	-	-
Shear force	8	S1	-	Breast	25.917 ± 2.4483	-	0.136 ± 0.0533	-	-
Shear force	8	S2	-	Thigh	30.175 ± 3.4533	-	0.136 ± 0.0533	-	-

[1]Empty boxes, denoted with (-), indicate that the effect is not included in the best prediction model. Parameter estimates for temperature represent the interaction between stress and temperature when stress type is specified. If stress type is not specified (-), then the interaction was not included in the best prediction model.
[2]Equations with the same model ID were parameterized within the same statistical model.
[3]Control = no treatment applied, Acute = TS for ≤24 h, Chronic = TS for >24 h.
[4]Average treatment temperature.
[5]Interaction between Species and Age in days when birds were slaughtered.
[6]Time in hour PM that the measurement was taken.

Table 7. Evaluation statistics for the best prediction equation determined by meta-analysis.

	Lightness (L*)	Redness (a*)	Yellowness (b*)	Initial pH	Ultimate pH	Drip loss (%)	Cooking loss (%)	Shear force (N)
Model ID	1	2	3	4	5	6	7	8
Observed								
Mean	51.12	6.25	7.07	6.17	5.92	1.56	21.78	28.98
SD	5.190	5.212	4.916	0.281	0.203	1.145	9.783	15.301
Predicted								
Mean	51.30	5.63	7.08	6.19	5.89	1.53	21.87	28.67
SD	4.606	4.008	4.824	0.247	0.105	1.082	9.440	14.548
RMSE (%)[1]	2.47 ± 0.173	2.30 ± 0.242	0.81 ± 0.131	0.09 ± 0.011	0.14 ± 0.006	0.20 ± 0.025	1.21 ± 0.1827	3.90 ± 0.375
ECT (%)[2]	1.4	7.4	0.01	3.1	3.3	2.2	0.5	0.7
ER (%)[3]	5.1	11.4	0.01	6.7	14.9	5.4	5.03	0.4
ED (%)[4]	93.4	81.2	99.9	90.2	81.8	92.3	94.5	98.9
CCC[5]	0.92 ± 0.007	0.86 ± 0.014	0.97 ± 0.005	0.92 ± 0.007	0.76 ± 0.005	0.98 ± 0.008	0.99 ± 0.002	0.94 ± 0.006
R[6]	0.956	0.918	0.983	0.957	0.783	0.986	0.993	0.967
C$_b$[7]	0.962	0.936	0.985	0.963	0.806	0.994	0.992	0.971
CV$_K$[8]	1.900	1.299	0.750	0.00484	0.00850	0.0128	1.455	13.195
Plots								
Intercept[9]	7.93 ± 1.065*	1.21 ± 0.201*	0.26 ± 0.128*	1.01 ± 0.156*	3.50 ± 0.158*	0.08 ± 0.039*	1.00 ± 0.276*	2.01 ± 0.926*
Slope[10]	0.08 ± 0.026*	0.19 ± 0.042*	0.002 ± 0.015	0.09 ± 0.033*	0.51 ± 0.100*	0.04 ± 0.023	0.03 ± 0.012±*	0.02 ± 0.031*

[1]Root mean square prediction error expressed as a percentage of the observed mean ± SD for all 5 k-folds.
[2]Error due to bias expressed as a percentage of MSPE.
[3]Error due to regression slope deviation expressed as a percentage of MSPE.
[4]Error due to disturbance expressed as a percentage of MSPE.
[5]Mean concordance correlation coefficient ± SD for all 5 K-folds.
[6]Pearson correlation coefficient.
[7]Bias correction factor.
[8]Test error based on the K-fold cross validation approach.
[9]Intercept of predicted versus observed regression. Values are presented as estimate ± SE and * indicates a significant difference from zero.
[10]Slope of residual versus predicted regression. Values are presented as estimate ± SE and * indicates a significant difference from zero.
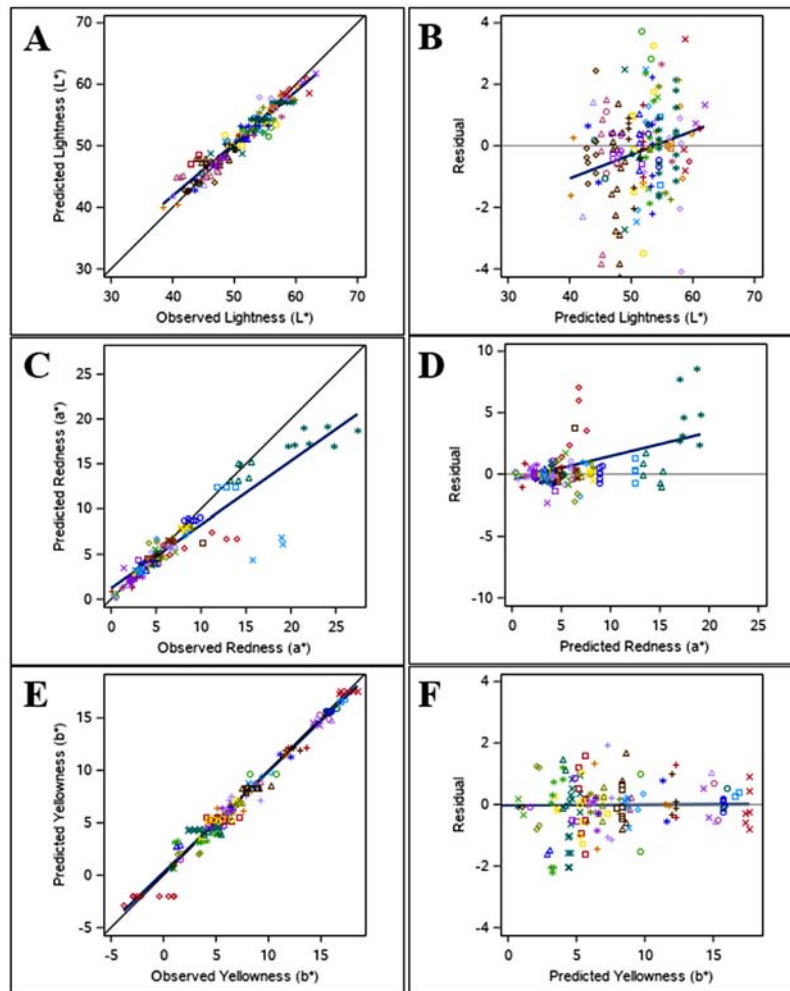
Figure 2. Predicted vs. observed and predicted vs. residual plots for the best prediction models for lightness (L*) (A and B), redness (a*) (C and D), and yellowness (b*) (E and F). Symbols that share the same shape and color are treatment means from the same study.

homogenous residual error distribution (Figure 2). The model developed indicates that the effect of temperature on L* differed between stress durations. With each degree increase in temperature under chronic stress conditions (>24 h), the L* value increases by 0.07 ± 0.021 (L3 and L6, Table 4), compared to a slope of 0.02 ± 0.015 under acute stress conditions (L2 and L5, Table 4) and a slope of 0.03 ± 0.015 under control conditions. In general, it was found that as slaughter age increases, L* is lower (darker meat) compared to younger broilers (L1−3, Table 4) and turkeys (L4−6, Table 4). There was also a significant influence of PM color measurement time on L* (Model 1, Table 4), with increased L* values over time indicating lighter meat as measurements were taken later.

Redness (a*) The best prediction model included the fixed effects of muscle type (breast vs. thigh; $P < 0.0001$) and temperature ($P < 0.05$) (Model 2, Tables 4 and 7). Model evaluation (Table 7) shows a low RMSPE (2.30%) with the majority of error coming from random sources (ED, 81.2%), a high CCC (0.86), and a CV_k of 1.3%, indicating good overall fit of the data and homogeneous residual error distribution (Figure 2). In general, thigh meat is more red (higher a*, R2, Table 4) than breast meat (R1, Table 4). It was found that as

treatment temperature increases, a* decreases by 0.02 ± 0.007 (Model 2, Table 4). Although the duration of TS was not included in the best prediction model, it was still shown to have a significant effect on a* ($P < 0.05$) with the largest effect observed under chronic stress conditions. Species was also found to have a significant effect on a* ($P < 0.05$), however, this effect was not included in the best prediction model for this trait. In general, though, broiler meat tends to have higher a* values than turkey meat.

Yellowness (b*) The best prediction model included only the fixed effect of temperature ($P < 0.05$) (Model 3, Tables 4 and 7). Model evaluation (Table 7) shows a low RMSPE (0.81%) with the majority of error coming from random sources (ED, 99.9%), a high CCC (0.97), and CV_k of 0.8%, indicating good overall fit of the data with a homogenous residual error distribution and no detected slope bias (Figure 2). An increase in treatment temperature was associated with a higher b* value (Model 3, Table 4). There was a significant effect of species on b* ($P < 0.05$), however, this was not included in the best prediction model for this trait. In general, broiler meat tended to have higher b* values than turkey meat. Temperature stress duration, muscle, and slaughter age did not significantly affect b* ($P > 0.05$).

pH Traits (Initial, Ultimate)

Initial pH The best prediction model included the fixed effects of slaughter age within species ($P < 0.05$), the effect of treatment temperature ($P < 0.05$), and the effect of PM measurement time ($P < 0.0001$) (Model 4, Tables 5 and 7). Model evaluation (Table 7) shows a low RMSPE (0.09%) with the majority of error coming from random sources (ED, 90.2%), a high CCC (0.92), and a CV_k of 0.005%, indicating good overall fit of the data and homogenous residual error distribution (Figure 3). A lower initial pH was observed when treatment temperature was higher (Model 4, Table 5). A significant effect of stress duration (acute vs. chronic) or muscle type (breast vs. thigh) was not found for initial pH ($P > 0.05$). In general, as slaughter age increased within broilers (PI1, Table 5) or turkeys (PI2, Table 5), the initial meat pH was lower. Additionally, the initial pH decreased by 0.002 ± 0.0001 units/min when the measurement time is delayed (Model 4, Table 5).

Ultimate pH The best prediction model included the fixed effect of muscle type (breast vs. thigh; $P < 0.0001$) and treatment temperature ($P < 0.0001$) (Model 5, Tables 5 and 7). Model evaluation (Table 7) shows a low RMSPE (0.14%) with the majority of error coming from random sources (ED, 81.8%), a moderate CCC (0.76), and a CV_k of 0.009%, indicating good overall fit of the data and homogeneous residual error distribution (Figure 3). In general, breast meat (PU1, Table 6) had a lower ultimate pH than thigh meat (PU2, Table 6). In terms of TS, it was found that as treatment temperature increased, ultimate pH decreased (Model 5, Table 5). The duration of TS was found to have a significant effect on ultimate pH ($P < 0.05$) but was not included in the best prediction model for this trait. Increasing the temperature under acute stress conditions lowered ultimate pH at a faster rate compared to chronic stress conditions. Species and slaughter age were not found to significantly affect ultimate pH ($P > 0.05$).

Drip Loss, Cooking Loss, and Shear Force

Drip Loss The best prediction model included the interaction between stress duration and treatment temperature ($P < 0.0001$) (Model 6, Tables 6 and 7). Model evaluation (Table 7) shows a low RMSPE (0.20%) with the majority of error coming from random sources (ED, 92.3%), a high CCC (0.98), and a CV_k of 0.01%, indicating good overall fit of the data with homogenous residual error distribution and no detected slope bias (Figure 4). As temperature increased, meat drip loss increased under all conditions. A higher increase was observed under chronic stress conditions (D3, Table 6), followed by acute stress conditions (D2, Table 6), whereas the smallest increase was observed in the control group (D1, Table 6). Species, slaughter age, and muscle were not found to have significant effects on meat drip loss ($P > 0.05$).

Cooking Loss The best prediction model included the fixed effects of muscle ($P < 0.0001$) and treatment temperature ($P < 0.05$) (Model 7, Tables 6 and 7). Model evaluation (Table 7) shows a low RMSPE (1.21%) with the majority of error coming from random sources (ED, 94.5%), a high CCC (0.99), and a CV_k of 1.5%, indicating good overall fit of the data and homogenous residual error distribution (Figure 4). In general, breast meat (C1, Table 6) tended to have a lower percent cooking loss than thigh meat (C2, Table 6). As treatment temperature increased by one degree, percent cooking loss increased by $0.045 \pm 0.0176\%$ (Model 7, Table 6). Temperature stress duration and slaughter age were found to
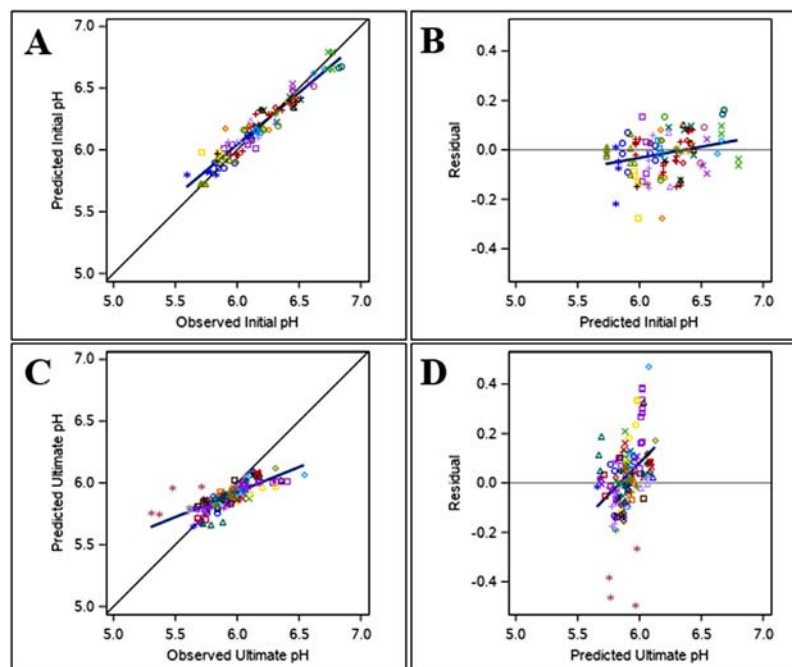

Figure 3. Predicted vs. observed and predicted vs. residual plots for the best prediction models for initial pH (A and B) and ultimate pH (C and D). Symbols that share the same shape and color are treatment means from the same study.
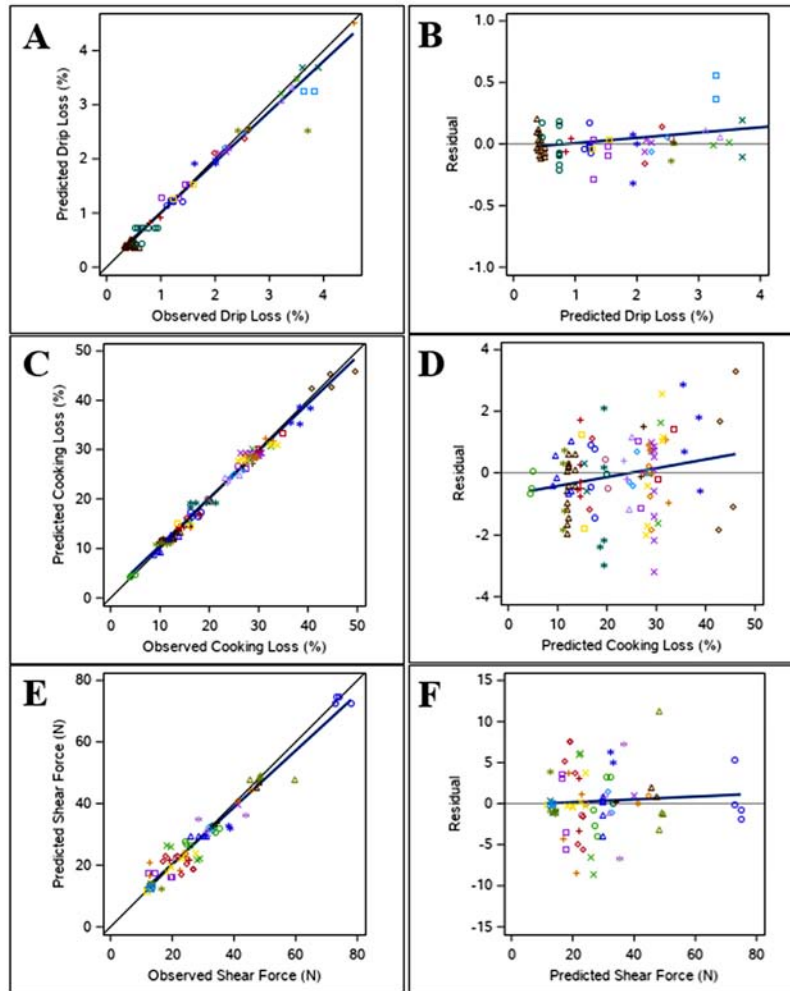
Figure 4. Predicted vs. observed and predicted vs. residual plots for the best prediction models for drip loss (%) (A and B), cooking loss (%) (C and D), and shear force (N) (E and F). Symbols that share the same shape and color are treatment means from the same study.

have significant effects on cooking loss ($P < 0.05$) but were not included in the best prediction model for this trait. The effect of increasing temperature on cooking loss was larger under acute stress conditions ($0.032 \pm 0.0258\%$) compared to chronic stress ($0.025 \pm 0.0221\%$). Regarding slaughter age, birds that were older at slaughter had meat with increased cooking loss ($0.033 \pm 0.0111\%$).

Shear Force The best prediction model included the fixed effects of muscle ($P < 0.0001$) and treatment temperature ($P < 0.05$) (Model 8, Tables 6 and 7). Model evaluation (Table 7) shows a low RMSPE (3.90%) with the majority of error coming from random sources (ED, 98.9%), a high CCC (0.94), and a CV_k of 13.2, indicating good overall fit of the data and homogenous residual error distribution (Figure 4). Thigh meat had a higher shear force than breast meat (S2 vs. S1, Table 6). Like drip loss and cooking loss, higher shear force was observed with increasing treatment temperature (Model 8, Table 6). Temperature stress duration (acute vs. chronic) and species (broiler vs. turkey) were found to have a significant effect on shear force ($P < 0.05$) but were not included in the best prediction model based on this database. Slaughter age did not have a significant effect on meat shear force ($P > 0.05$).

Separation of Heat and Cold Stress

Based on the results of the meta-analysis, a subanalysis was conducted to examine and consider heat stress vs. cold stress. Overall, they were found to differently affect the quality of poultry meat (Table 8). Treatment temperature for the cold stress and heat stress studies ranged from −18 to 24°C and 18 to 42°C, respectively. Meat lightness (L*) was significantly different between heat-stressed and cold-stressed birds ($P = 0.0001$). The average meat L* for heat-stressed birds was 52.14 ± 0.750, whereas the average L* for cold-stressed birds

Table 8. Results of heat stress (HS) vs. cold stress (CS) subanalysis: LSMeans ± SD for the meat quality traits of birds exposed to either heat stress (HS) or cold stress (CS) as reported in the studies included in the meta-analysis database.

Trait	HS	N	CS	N	P-value
Lightness (L*)	52.14 ± 0.750	86	50.55 ± 0.810	36	0.0001
Redness (a*)	5.49 ± 0.557	67	6.19 ± 0.574	36	0.0003
Yellowness (b*)	7.63 ± 0.784	66	7.58 ± 0.796	36	0.9723
Initial pH	6.19 ± 0.058	76	6.23 ± 0.071	8	0.6834
Ultimate pH	5.95 ± 0.023	65	6.02 ± 0.026	28	0.0010
Drip loss (%)	2.39 ± 0.252	38	2.14 ± 0.256	13	0.0003
Cooking loss (%)	24.57 ± 1.737	49	24.28 ± 1.783	22	0.8397
Shear force (N)	32.35 ± 3.072	43	32.67 ± 3.698	14	0.9902

was 50.55 ± 0.810. Meat redness (a*) was also found to be significantly different between the temperature treatments (5.49 ± 0.557 (heat) vs. 6.19 ± 0.574 (cold), $P = 0.0003$). However, there was no significant difference found in meat yellowness (b*) between the groups ($P > 0.05$).

No significant difference was found in the initial pH between heat-stressed and cold-stressed birds ($P > 0.05$), although it was found that the initial pH of meat from heat-stressed birds was significantly lower than that of birds raised at control temperatures (data not shown, $P = 0.0018$). However, a significant difference was found in meat ultimate pH between heat-stressed and cold-stressed birds ($P = 0.001$). Birds from cold-stress treatments had a significantly higher ultimate pH (6.015 ± 0.0263) than birds from heat-stress treatments (5.95 ± 0.0226).

A significant difference in mean drip loss was found between heat-stressed and cold-stressed birds ($P = 0.0003$). Birds in heat-stress treatments had a higher average drip loss ($2.39 \pm 0.252\%$) compared to birds in cold-stress treatments (2.14 ± 0.256). However, no similar relationship was found for cooking loss between the groups ($P > 0.05$). Additionally, there was no significant difference in shear force values ($P > 0.05$), however, there was a trend for heat-stressed birds to have a significantly higher shear force than birds raised at control temperatures ($P = 0.08$).

DISCUSSION

Temperature and Meat Quality

Across a large database of published literature, ambient temperature had an effect on all studied meat quality traits. As treatment temperature increased (heat stress), meat tended to be lighter (L*), less red (a*), and more yellow (b*), as well as having a lower initial and ultimate pH, and increased drip loss, cooking loss, and shear force. These results are in line with knowledge on the development of PSE-like meat under heat stress conditions and DFD-like meat under cold stress conditions but quantifies the effect across the body of literature available.

An increase in temperature has previously been shown to increase glycogen breakdown and subsequent acidification and degradation of muscle protein (Pietrzak et al., 1997; King and Whyte, 2006; Owens et al., 2009; Carvalho et al., 2014), while lower temperatures have been shown to counter this effect by causing depletion of glycogen stores prior to slaughter (Lee et al., 1976; Haman et al., 2002,2005; Dadgar et al., 2011,2012b). The fast acidification of PSE meat and degradation of muscle protein and pigments can explain the lower initial and ultimate pH as well as the color fading (higher L*, higher b*, lower a*), and decreased WHC (increased drip and cooking loss) at higher temperatures.

Overall, the prediction equations developed fit the data well based on the model evaluation measures.

The RMSPE% was low and for all equations most of the error could be attributed to random disturbance. The CCC values ranged between 0.76 and 0.99 which indicate that the observed and predicted values are closely related. The model test error (CV_K) was less than 2% for most models which indicate that the developed models are robust. The model for shear force had the highest CV_K (13.2%) which can likely be attributed to the smaller sample size for this trait (N = 90). The plots of predicted vs. observed values indicate good overall fit for most models, except for ultimate pH, which is reflected in the lowest calculated CCC (0.76). A significant slope bias ($P < 0.05$) was detected for all models except for b* and drip loss. After examination of the predicted vs. residual plots, this bias is potentially due to outlier studies and the fact that the random effect of study is not considered in the regression (PROC REG) analysis used to compare overall predicted vs. residual plots. To be as comprehensive as possible, we did not apply a temporal restriction to our search strategy, however, it may be advisable for future meta-analyses to consider applying a restriction (e.g., last 10 yr) to potentially avoid studies which are outliers because of changes in techniques or genetic selection.

Indicator Traits for Meat Quality Defects

To classify poultry meat quality defects, traits such as meat color and pH are used due to their relative ease of measurement and close relationship with each other, as well as to other relevant traits such as WHC and texture (Barbut, 1998; Owens et al., 2000a; Garcia et al., 2010; Dadgar et al., 2012b). The results of this meta-analysis support the use of both color and pH as indicators for meat quality parameters. In terms of color, we found that L*, and to a lesser extent a* and b*, were significantly correlated with meat quality traits such as pH, drip loss, and cooking loss (Table 3). Furthermore, we found a significant correlation between L* and a* and b* (Table 3). This could explain why a* and b* are not often used to classify PSE meat, as some say that they are largely redundant, and differences in L* tend to be larger. In any case, measuring L* alone has been shown to be reliable at identifying PSE meat (Barbut, 1993; Petracci et al., 2004) and the relationship between a* or b* and other indicator traits (e.g., ultimate pH) are not always as well established in the literature. This could suggest that recording a single value for L* (which today can be done inline at high speed) might be more efficient than additionally assessing a* and b* values. In terms of pH to classify PSE meat in poultry, ultimate pH appears to be a more valid indicator of meat quality defects than initial pH (Garcia et al., 2010; Eadmusik et al., 2011). This could be supported by the results of this meta-analysis, as ultimate pH was correlated with more of the relevant meat quality parameters (i.e., L*, drip loss, and cooking loss) compared to initial pH which was only correlated to cooking loss (Table 3).

Implications for Consumer Acceptance

Our analysis showed that birds exposed to higher temperatures are more likely to produce meat with PSE-like characteristics, whereas birds exposed to colder temperatures are more likely to produce meat with DFD-like characteristics. These characteristics are unappealing to consumers and could have negative implications for the profitability of the industry. We were able to show that ambient TS can significantly affect meat color. Although there may be no classifiable defect, meat color is highly related to consumer acceptance, and is considered one of the most important characteristics at the point of purchase (West et al., 2001; Banović et al., 2009). Meat color is particularly relevant today, as most cut-up poultry is sold in trays covered with clear plastic film (Min and Ahn, 2012; Font-i-Furnols and Guerrero, 2014). Western consumers have been shown to react negatively when chicken meat has a yellow color, and were more likely to act favorably when the yellow color was disguised (Kennedy et al., 2005). Our analyses showed that increasing temperature was more likely to result in paler and more yellow meat. Additionally, with increasing temperature, drip loss, cooking loss, and shear force all showed higher values. Drip and cooking losses are important indicators of WHC. Poor WHC detracts from the product's appearance, reduces the weight of fresh meat, and can impact the juiciness of the meat once it is cooked. Meat that loses a significant amount of moisture while cooking may result in a cooked product that is dry, less tender and is less preferred by consumers (Warriss, 2000).

Separation of Heat vs. Cold Stress

The results of the subanalysis are similar to the regression equations developed for TS and indicate that hot and cold conditions may differently affect some poultry meat quality traits. Birds undergoing heat stress treatments tended to have meat that was lighter and less red, with a lower ultimate pH and higher drip loss compared to cold stress. This is similar to the findings of many published studies and reviews which attribute PSE meat to heat stress conditions and DFD meat to cold stress conditions (Bianchi et al., 2006; Barbut et al., 2008; Gonzalez-Rivas et al., 2020). However, these results should be interpreted with some caution given the relative imbalance between heat and cold studies included, as well as the unequal distribution of studies assessing cold stress between species ($N_{Broiler}=9$, $N_{Turkey}=3$). It is possible that with more cold stress studies considered, the results of this analysis could change.

Acute vs. Chronic Stress

Acute TS is typically designed to mimic the effect of temperature during short-term or daily fluctuations soon before slaughter (i.e., during transportation or lairage), whereas chronic TS simulates the effect of temperature during long-term or seasonal changes that can occur during production. The interaction between treatment temperature and duration of TS (acute vs. chronic) was only included in the best prediction model for 2 traits (L* and drip loss), but was also found to be significant ($P < 0.05$) for all other traits except for yellowness and initial pH.

Based on our analysis, there was no clear consensus as to whether acute or chronic TS has a larger effect on meat quality traits in poultry. Acute stress had a larger effect on ultimate pH, cooking loss, and shear force, compared to chronic stress which had a larger effect on color (L* and a*) and drip loss. From this, we could suggest that acute exposure to extreme temperatures soon before slaughter is more likely to have larger impact on pH traits, whereas chronic exposure to TS is more likely to have a larger impact on meat color.

It is possible that the inconsistent effect magnitude between acute and chronic stress on the studied meat quality traits is due to the varying range of temperatures within the acute and chronic categories used here. The ranges in treatment temperatures for the acute and chronic categories (within this meta-analysis) were −18 to 42°C and 15 to 36°C, respectively, with medians of 34°C and 34°C, respectively. Overall, more extreme temperatures are represented within the acute category, whereas more moderate temperatures are in the control and chronic categories. To be as comprehensive as possible, studies were not excluded from the meta-analysis based on their treatment temperature. Future studies may discern the effects of acute and chronic temperature exposure when temperature ranges are more similar. Additionally, the range of TS exposure time varied considerably within the acute and chronic categories. Within acute stress (≤24 h), the actual duration of exposure in the various studies ranged from 20 min to 24 h before slaughter. Within chronic stress (>24 h), the actual duration of exposure in the various studies ranged from 3 to 70 d. It is possible that the large range of exposure times within these categories contributed to the differing relative effect magnitude of acute and chronic stress on meat quality traits, though they could be representative of what occurs in practice. Recategorization of the treatment duration or using treatment duration as a continuous variable may help clarify this relationship in future studies.

Of importance, not all birds are PSE-susceptible under heat stress conditions. Stress-susceptibility is well documented in pigs, and it has been shown that susceptible pigs are more likely to develop PSE meat than non-susceptible animals (Offer, 1991). In pigs, a point mutation in the RYR1 gene (ryanodine receptor) has been determined as the genetic cause of malignant hyperthermia resulting in PSE meat (Fujii et al., 1991; Paiao et al., 2013). In chickens and turkeys, RYR1 polymorphisms and variants in RYR1 transcripts have been discovered but were not related to the development of PSE meat, so the genetic cause for this myopathy in poultry remains unknown (Chiang et al., 2004; Droval et al., 2012). Although the cause has not been identified, it is possible that some birds within a given

study treatment are susceptible to PSE meat and others are not, which could result in variation in effect magnitude between studies.

Practical Significance

Although TS was demonstrated to have a significant effect on meat quality parameters, it must be discussed whether these effects are practically significant from a meat production perspective. In general, with increasing or decreasing temperature, the parameter estimates for the effect of temperature on meat quality traits were low. To illustrate, reported L* cut-offs for PSE meat can range between 49 and 56 depending on the study (Petracci et al., 2009), or poultry meat having an ultimate pH of <5.8 has also been used in practice (Garcia et al., 2010). If we assume an L* cut-off of 53, in the middle of the range, a broiler slaughtered at 42 d of age would have to be chronically exposed to 30°C or greater, or acutely exposed to 75°C or greater to have an L* value greater than 53, based on (linear) extrapolation of the prediction equations. For ultimate pH, a bird would need to be exposed to temperatures over 50°C for ultimate pH to drop below 5.8. While chronic exposure to 30°C may be plausible, exposure to temperatures greater than 50°C are unlikely in most production systems. It is, however, possible that these temperatures could be reached acutely during transportation or heat waves in poultry operations in hot climates or when the apparent temperature (i.e., combination of high air temperature with low air velocity, high humidity, and high stocking density) is considered. Humidity is especially important to consider for poultry, which are especially poor at dissipating heat and panting is less effective under high humidity conditions (Jahejo et al., 2016; van Dyk et al., 2019). Unfortunately, only 19 of the 48 studies reported relative humidity so we did not include this variable in the analysis, although it undoubtedly influences heat stress. Including aspects of 'apparent' temperature should be the focus of future studies or meta-analyses.

Heat stress impairs the performance of poultry by reducing feed intake and increasing the feed conversion ratio, with ultimately slower growth (Lara and Rostagno, 2013; Habibian et al., 2014; Tawfeek et al., 2014). An estimate from 2003 indicates that economic losses from heat stress in the US poultry industry can amount to $128 million annually (St-Pierre et al., 2003). This could indicate that the greatest impact of TS may be its effect on body weight gain/efficiency and not its impact on meat quality, since it appears to take extreme temperature conditions to result in a classifiable defect based on the results of this meta-analysis. However, since body and muscle growth is undoubtedly connected to meat quality (Dransfield and Sosnicki, 1999), these effects are not necessarily independent, especially in the case of chronic exposure over the growing period (i.e., seasonal heat stress). Furthermore, the extrapolation of our prediction equations assumes a continuous linear relationship between temperature and meat quality traits. The relationship may be nonlinear, and so extrapolations of these equations beyond the breadth of the developmental database (temp range: −8 to 42°C) may not be accurate. Regardless, even if the effects of temperature on meat quality do not result in classifiable defects, they may still negatively affect consumer acceptance of the product and are certainly relevant for welfare.

CONCLUSIONS

The results of this meta-analysis demonstrate that TS significantly affects each of the studied meat quality traits. Furthermore, we also show that these effects can be numerically quantified across a large database of published studies. In brief, it was found that as overall treatment temperature increases, poultry meat has a tendency to be lighter (L*), less red (a*), and more yellow (b*), as well as having a lower initial and ultimate pH, and increased drip loss, cooking loss, and shear force. Conversely, birds exposed to colder temperatures are more likely to produce meat that is darker, redder, and less yellow, as well as having a higher initial and ultimate pH, and decreased drip loss, cooking loss, and shear force. This meta-analysis quantifies previously published research describing heat stress induced PSE meat and cold stress induced DFD meat in poultry. Significant effects of temperature were found for all examined traits; however, the effect magnitude is generally small. Future studies should perform a separate analysis of heat stress and cold stress to better examine the effect of duration or analyze the impact of effective temperature (including air velocity, humidity, stocking density, etc.).

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DISCLOSURES

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