


RESEARCH

Open Access



A behavior and physiology-based decision support tool to predict thermal comfort and stress in non-pregnant, mid-gestation, and late-gestation sows

Betty R. McConn¹, Allan P. Schinckel², Lindsey Robbins², Brianna N. Gaskill², Angela R. Green-Miller³, Donald C. Lay Jr.⁴ and Jay S. Johnson^{4*} 

Abstract

Background: Although thermal indices have been proposed for swine, none to our knowledge differentiate by reproductive stage or predict thermal comfort using behavioral and physiological data. The study objective was to develop a behavior and physiology-based decision support tool to predict thermal comfort and stress in multiparous (3.28 ± 0.81) non-pregnant ($n = 11$), mid-gestation ($n = 13$), and late-gestation ($n = 12$) sows.

Results: Regression analyses were performed using PROC MIXED in SAS 9.4 to determine the optimal environmental indicator [dry bulb temperature (T_{DB}) and dew point] of heat stress (HS) in non-pregnant, mid-gestation, and late-gestation sows with respiration rate (RR) and body temperature (T_B) successively used as the dependent variable in a cubic function. A linear relationship was observed for skin temperature (T_S) indicating that T_{DB} rather than the sow HS response impacted T_S and so T_S was excluded from further analyses. Reproductive stage was significant for all analyses ($P < 0.05$). Heat stress thresholds for each reproductive stage were calculated using the inflections points of RR for mild HS and T_B for moderate and severe HS. Mild HS inflection points differed for non-pregnant, mid-gestation, and late gestation sows and occurred at 25.5, 25.1, and 24.0 °C, respectively. Moderate HS inflection points differed for non-pregnant, mid-gestation, and late gestation sows and occurred at 28.1, 27.8, and 25.5 °C, respectively. Severe HS inflection points were similar for non-pregnant and mid-gestation sows (32.9 °C) but differed for late-gestation sows (30.8 °C). These data were integrated with previously collected behavioral thermal preference data to estimate the T_{DB} that non-pregnant, mid-gestation, and late-gestation sows found to be cool ($T_{DB} < T_{DB}$ preference range), comfortable ($T_{DB} = T_{DB}$ preference range), and warm (T_{DB} preference range $< T_{DB} <$ mild HS).

Conclusions: The results of this study provide valuable information about thermal comfort and thermal stress thresholds in sows at three reproductive stages. The development of a behavior and physiology-based decision support tool to predict thermal comfort and stress in non-pregnant, mid-gestation, and late-gestation sows is expected to provide swine producers with a more accurate means of managing sow environments.

Keywords: Decision support, Gestation, Heat stress, Management, Sows, Thermal index

Background

Heat stress (HS) is a threat to swine productivity, health, and welfare [1–3] that will become increasingly common as global temperatures continue to rise and extreme

*Correspondence: jay.johnson2@usda.gov

⁴ USDA-ARS Livestock Behavior Research Unit, West Lafayette, IN 47907, USA
Full list of author information is available at the end of the article



© The Author(s) 2022. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>. The Creative Commons Public Domain Dedication waiver (<http://creativecommons.org/publicdomain/zero/1.0/>) applies to the data made available in this article, unless otherwise stated in a credit line to the data.

climatic events increase in frequency [4, 5]. Furthermore, the negative effects of global climate change and increasing environmental heat loads on animal agriculture may be exacerbated by advances in genetic selection, nutrition, and management that have increased pig performance leading to more efficient meat production, faster growth rates, and greater lactation outputs by sows to support greater litter sizes [6–8]. While these advancements promote agricultural sustainability and producer profitability, improved performance has resulted in greater overall metabolic heat production in modern swine [9]. This increase in metabolic heat production may be exacerbated by physiological states such as lactation [10, 11] or gestation [12], and reduces the thermal gradient between the pig and the external environment [13]. As a result, HS susceptibility is likely greater, which can negatively impact health and productivity and, subsequently, may reduce the performance, health, and welfare of future generations of pigs through in utero heat stress (IUHS) [3, 14].

Research by our group and others demonstrates that IUHS reduces postnatal productivity, health, and welfare in pigs [3, 14], and has negative implications for swine industry profitability and sustainability. Specifically, IUHS reduces postnatal growth performance [15, 16], increases the prevalence of behaviors indicative of stress (e.g., aggression, lying) during postnatal life [17, 18], exacerbates physiological indicators of stress (i.e., cortisol, ACTH) following common production stressors [18–21], reduces the ability of pigs to maintain euthermy under HS conditions [22, 23], impairs reproductive function [24], and compromises the immune system of pigs during postnatal life [19, 25]. While some studies have unsuccessfully attempted to mitigate the negative effects of IUHS through nutritional strategies [16], pregnant sow management and HS mitigation during gestation likely represents the best method to decrease IUHS incidence and improve the postnatal performance, health, and welfare of pigs gestated during hot times of the year.

The first step in mitigating gestating sow HS and the effects of IUHS in offspring is understanding what environmental conditions cause HS in gestating sows. Currently, there are recommended thermal conditions for swine at different production stages [26]. However, these guidelines are based upon 25- to 41-year-old data estimating the thermal conditions of pigs using mathematical modeling [13] based on previous research [27, 28] rather than animal experimentation. Furthermore, no reproductive stage differentiation exists (i.e., non-pregnant/early gestation vs. mid-gestation vs. late-gestation) [26], which is important because gestation stage impacts sow HS sensitivity [29–31]. In addition, while several researchers have utilized the thermal humidity

index (THI) developed by NOAA [32] to predict HS in pigs [33–35], this index was not originally designed for use in pigs, nor does it differentiate HS thresholds based on production stage or physiological state. Thus, THI may not be an accurate and precise predictor of HS in swine. Furthermore, although several swine specific thermal indices or prediction models have been proposed in recent years, these indices rely on the use of theoretical data or predictions [36–38] with validations on a small number ($n=8$) of animals [39], or limited data collection in a relatively small number of only non-pregnant sows [40], and none to our knowledge have incorporated both behavioral and physiological metrics of thermal stress and thermal comfort in pigs differentiated by reproductive stage. Therefore, the study objective was to develop a swine-specific decision support tool to predict thermal comfort and stress based on the thermoregulatory and behavioral responses of sows with current genetics at three reproductive stages (e.g., non-pregnant, mid-gestation, late-gestation).

Methods

Establishing mild, moderate, and severe HS thresholds

Thermoregulatory data collection

All live animal data collection procedures were approved by the Purdue University Animal Care and Use Committee (protocol # 1811001823). Animal care and use standards were based upon the *Guide for the Care and Use of Agricultural Animals in Research and Teaching* [41]. All data collection procedures and resulting thermoregulatory, production, and physiological data have been previously presented by McConn et al. [31]. For the purposes of this paper, only the environmental [e.g., dry bulb temperature (T_{DB}), dew point (DP)] and thermoregulatory [e.g., skin temperature (T_S), respiration rate (RR), and body temperature (T_B)] measures from McConn et al. [31] were considered for the analyses. Briefly, 36 maternal line sows (Yorkshire \times Landrace) bred to Duroc sires were tested in 4 repetitions that began and ended at the same approximate time each day. Treatment groups included sows from three reproductive stages: 11 non-pregnant sows ($n=2$ –3/repetition; parity 3.27 ± 0.86 ; 244.2 kg bodyweight), 13 mid-gestation sows ($n=3$ –4/repetition; 56.38 ± 11.22 d pregnant; parity 3.25 ± 0.83 ; 218.9 kg bodyweight), and 12 late-gestation sows ($n=3$ /repetition; 97.00 ± 4.95 d pregnant; parity 3.33 ± 0.75 ; 251.2 kg bodyweight). Early gestation sows were not included as a treatment group because it was expected that their response would be similar to non-pregnant sows due to limited fetal growth in the first trimester, which is the driver of HS sensitivity differences in gestating sows [31]. Sows were moved into individual pens (1.22 m \times 2.01 m) in a thermoneutral [TN; 21.1 ± 2.0 °C

and $29.4\% \pm 1.6\%$ relative humidity (RH)] room for 5.0 ± 0.7 d prior to the experiment [31]. At the start of the experiment, sows were moved (approximately 3 m walking distance) [42] into individual pens ($1.22 \text{ m} \times 2.01 \text{ m}$) within an environmentally controlled room where they were maintained at the lower end of the currently established TN zone for sows $> 100 \text{ kg}$ [4] ($15.1 \pm 1.9 \text{ }^\circ\text{C}$ and $50.7\% \pm 5.6\%$ RH) for 270 min prior to the experiment and allowed to acclimate to their new environment. At the time of the experiment, the T_{DB} was increased gradually from $19.84 \pm 2.15 \text{ }^\circ\text{C}$ to $35.54 \pm 0.43 \text{ }^\circ\text{C}$, over a 400-min period and RH ranged from 32.83% to 50.13% and averaged $40.49\% \pm 18.57\%$. The environmental room contained 2 data loggers (Hobo; data logger temperature/RH; accuracy $\pm 0.20 \text{ }^\circ\text{C}$; Onset; Bourne, MA, USA) to record T_{DB} , RH, and DP in 5-min intervals as previously described [31]. Room air speed (m/s) was measured with an anemometer (Testo Model 425; Sparta, NJ, USA) at the pig level (approximately 0.50 m above the slatted floor) every 20 min during the entire experiment and measured $0.11 \pm 0.10 \text{ m/s}$ throughout the trial. Vaginal temperature (referred to as T_B in the present paper), T_S , and RR were measured in 20-min intervals for all sows and measurement methods were previously described by McConn et al. [31]. Briefly, T_B was collected using a calibrated thermochron temperature recorder (iButton, calibrated accuracy $\pm 0.11 \text{ }^\circ\text{C}$; resolution = $0.125 \text{ }^\circ\text{C}$; Dallas Semi-conductor, Maxim, Irving, TX, USA), T_S was measured using an infrared camera (FLIR Model T440, accuracy $\pm 2\%$; emissivity = 0.98;

resolution = $0.04 \text{ }^\circ\text{C}$; FLIR Systems Inc.; Wilsonville, OR, USA), and RR was determined by counting flank movements through visual observation. The DP and T_{DB} that occurred at the exact time T_S , T_B , and RR were measured were used to establish the HS thresholds in the analyses. All sows, regardless of reproductive stage, were limit fed to maintenance (2.27 kg/d) resulting in no feed intake differences between sow groups per common commercial swine production practices [43] as previously described [31].

Overall regression analyses

Regression analyses were performed to determine the optimal environmental indicator of HS in non-pregnant, mid-gestation, and late-gestation sows using the linear model procedure with all animal-based indicators successively used as dependent variables. The base model for modeling the animal-based indicators included the effects of T_S , T_B , and RR. Skin temperature had a linear relationship with increasing T_{DB} , regardless of reproductive stage (Fig. 1) [31]. Therefore, T_S was not included in further analyses because this linear relationship was influenced by increasing environmental heat load rather than the sows' biological HS response or reproductive stage. Regression analyses were then performed, and several combinations of environmental measures (T_{DB} and DP) were added to the model when significant ($P < 0.05$; Table 1). The goodness of fit of the regression equations was evaluated by the Akaike's Information Criteria (AIC) and residual variance based upon previous research [44–47].

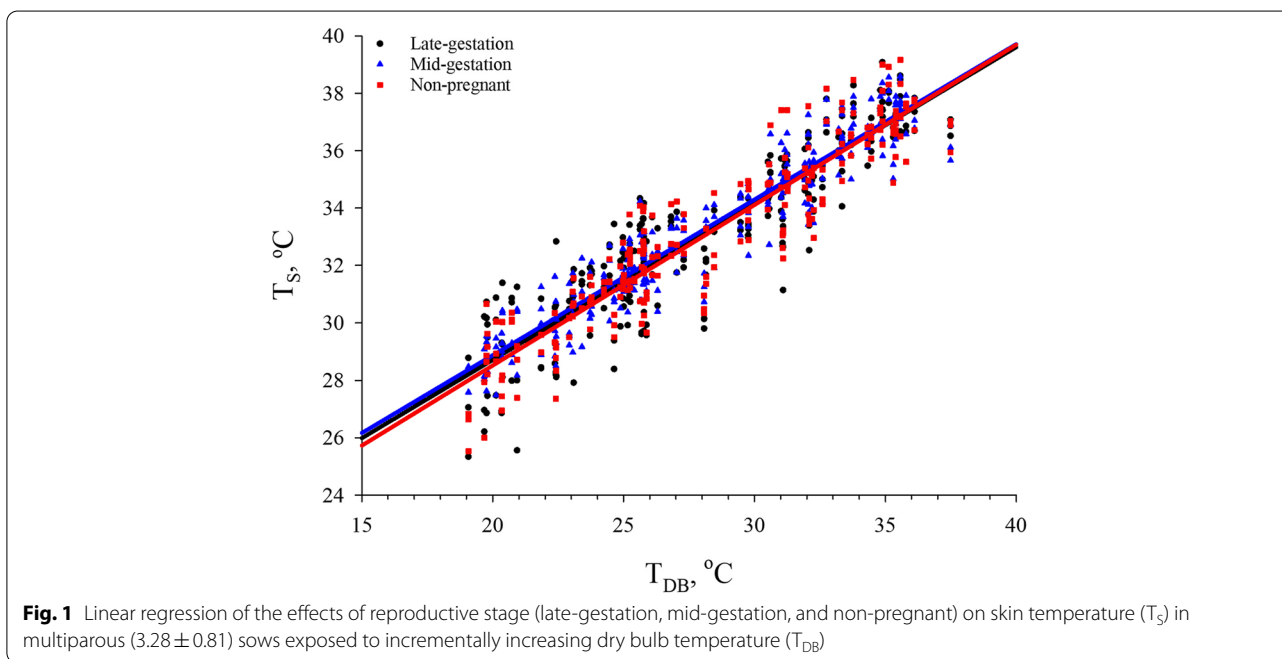


Table 1 Evaluation of regression model fit after inflection point determination

| Parameter | AIC | Residual variance | P-value |
|------------------------------------|---------|-------------------|---------|
| Inflection point of T_{DB} | | | |
| Mild HS | | | |
| Late-gestation | 1914.00 | 109.66 | 0.01 |
| Mid-gestation | 1899.00 | 46.49 | 0.02 |
| Non-pregnant | 1589.50 | 47.83 | < 0.01 |
| Moderate HS | | | |
| Late-gestation | -28.90 | 0.03 | 0.04 |
| Mid-gestation | -46.20 | 0.03 | 0.02 |
| Non-pregnant | 76.00 | 0.06 | 0.01 |
| Severe HS | | | |
| Late-gestation | -28.90 | 0.03 | 0.03 |
| Mid-gestation | -46.20 | 0.03 | < 0.01 |
| Non-pregnant | 76.00 | 0.06 | 0.01 |
| T_{DB} minus T_{DB} breakpoint | | | |
| Mild HS | | | |
| Late-gestation | 1888.80 | 88.17 | 0.04 |
| Mid-gestation | 1851.40 | 45.57 | 0.04 |
| Non-pregnant | 1542.20 | 42.90 | 0.02 |
| Moderate HS | | | |
| Late-gestation | -52.30 | 0.02 | < 0.01 |
| Mid-gestation | -57.80 | 0.03 | 0.02 |
| Non-pregnant | 42.40 | 0.05 | 0.03 |
| Severe HS | | | |
| Late-gestation | -41.50 | 0.01 | 0.01 |
| Mid-gestation | -69.70 | 0.02 | 0.04 |
| Non-pregnant | 38.30 | 0.04 | 0.04 |
| Inflection point of DP | | | |
| Mild HS | | | |
| Late-gestation | 1918.10 | 106.99 | < 0.01 |
| Mid-gestation | 1889.00 | 44.07 | < 0.01 |
| Non-pregnant | ND | ND | 0.67 |
| Moderate HS | | | |
| Late-gestation | -33.20 | 0.03 | 0.01 |
| Mid-gestation | -53.30 | 0.03 | 0.02 |
| Non-pregnant | ND | ND | 0.21 |
| Severe HS | | | |
| Late-gestation | -41.50 | 0.01 | < 0.01 |
| Mid-gestation | -69.70 | 0.02 | < 0.01 |
| Non-pregnant | ND | ND | 0.22 |
| DP minus DP breakpoint | | | |
| Mild HS | | | |
| Late-gestation | 1855.60 | 84.38 | 0.03 |
| Mid-gestation | 1823.90 | 21.67 | 0.02 |
| Non-pregnant | ND | ND | 0.54 |
| Moderate HS | | | |
| Late-gestation | -59.00 | 0.02 | < 0.01 |
| Mid-gestation | -65.60 | 0.03 | < 0.01 |
| Non-pregnant | ND | ND | 0.87 |
| Severe HS | | | |
| Late-gestation | -66.90 | 0.01 | 0.01 |
| Mid-gestation | -70.40 | 0.01 | 0.02 |
| Non-pregnant | ND | ND | 0.43 |

T_{DB} Dry bulb temperature, HS Heat stress, DP Dew point, ND Not determined

Separating reproductive stage

The first analysis was conducted using the data set that included the reproductive stages together to evaluate means, variances, and the relationships of RR and T_B in sows at different reproductive stages to increasing T_{DB} using the MIXED procedure of SAS (SAS 9.4, Cary, NC, USA) with a heterogeneous AR(1) covariance structure which was selected based on the AIC value (compares the fit of the covariance structures) [48]. Reproductive stage was significant for linear, quadratic, and cubic analyses ($P < 0.05$; Table 2); thus, reproductive stage was separated for future analyses.

Random effect of sow

In the second analysis, before separating sow by reproductive stage, the random effect of sow was tested to determine whether it would improve the model, based on the AIC and residual variance. A random effect of sow allows for increased flexibility in fitting the sow variance in the RR and T_B curves. Since the addition of sow as a random effect improved the AIC and residual variance (Table 3), the random effect of sow was used for all future analyses.

Random effect of T_{DB}

The third analysis was performed to determine how the random effect of T_{DB} would be included to account for the correlation with the individual sow (subject = sow). The random effect was first included as the intercept (B_0) and then included as B_0 and linear regression coefficient (B_1) based on the AIC and residual variance. Since the AIC and residual variance was improved when the random effect was included as B_0 and B_1 (Table 3), this was used for the remainder of the analyses. Note, in most cases AIC values are positive; however, in some cases the AIC value can be impacted by an additive constant resulting in a negative AIC value [49].

Determination of inflection points

The fourth analysis began by separating the reproductive stage to estimate the environmental measure (T_{DB}) as a linear, quadratic, or cubic function for RR and T_B based on the AIC and residual variance. These functions

Table 2 Evaluating the significance of the interaction of reproductive stage and the linear, quadratic, and cubic regression of T_{DB}

| Parameter | P-value |
|--|---------|
| Reproductive stage $\times T_{DB}$ | 0.04 |
| Reproductive stage $\times T_{DB} \times T_{DB}$ | 0.03 |
| Reproductive stage $\times T_{DB} \times T_{DB} \times T_{DB}$ | < 0.01 |

T_{DB} Dry bulb temperature

Table 3 Evaluation of regression model fit

| Parameter | AIC | Residual variance |
|--|---------|-------------------|
| Testing sow as random | | |
| Without sow as random | | |
| RR | 5855.60 | 140.51 |
| T _B | 815.20 | 0.19 |
| With sow as random | | |
| RR | 5451.50 | 67.91 |
| T _B | 5.50 | 0.04 |
| Testing random effects before inflection point | | |
| Random as B ₀ | | |
| RR | | |
| Late-gestation | 1962.50 | 137.98 |
| Mid-gestation | 1968.80 | 66.30 |
| Non-pregnant | 1692.50 | 80.62 |
| T _B | | |
| Late-gestation | 11.00 | 0.05 |
| Mid-gestation | 39.00 | 0.05 |
| Non-pregnant | 110.10 | 0.08 |
| Random as B ₀ and B ₁ | | |
| RR | | |
| Late-gestation | 1914.00 | 109.66 |
| Mid-gestation | 1899.00 | 46.49 |
| Non-pregnant | 1589.50 | 47.83 |
| T _B | | |
| Late-gestation | -28.90 | 0.03 |
| Mid-gestation | -46.20 | 0.03 |
| Non-pregnant | 76.00 | 0.06 |

RR Respiration rate, T_B Body temperature

were used to describe the sow’s response of RR and T_B to changes in the T_{DB}. Next, we estimated the inflection points for both variables based on the determined functions and including breakpoint analyses [50]. Specifically, PROC MIXED allowed for inclusion of the random (sow) component in the model with a heterogeneous AR(1) covariance structure to determine the inflection points. Based on the AIC and residual variance (Table 1), T_{DB} minus T_{DB} inflection point was used in the final model. Physiological differences between treatment groups were analyzed using generalized linear mixed models via PROC MIXED with the main effect of the variable (RR or T_B). A cubic equation was used to describe the RR and T_B response due to increasing T_{DB}. The inflection point was solved by finding value at which the RR or T_B started to increase via breakpoint analyses. The RR inflection point was used to determine mild HS because greater RR is the first active attempt by the sow to dissipate excess heat gain due to the environmental heat load [51, 52]. To determine moderate HS, the T_B inflection point was used as an indicator of the T_{DB} at which heat loss mechanisms

(i.e., RR and T_S) could no longer allow the sow to maintain eutheria under a given environmental heat load and the T_B set-point was increased above normal as described by Curtis [13]. Finally, an abrupt uncontrollable change in T_B (>0.20 °C) [53] after the inflection point indicated that heat gain overwhelmed heat loss mechanisms and T_B began to rise uncontrollably. This was considered the point at which the upper critical temperature limit had been reached and severe HS began to occur as previously described by Curtis [13]. Based on the AIC and residual variance (Table 3), T_{DB} minus T_{DB} inflection point was used for the final analysis. Once the inflection points were detected, the points less than or equal to the inflection point were reanalyzed to confirm there was no linear increase of the variable relative to T_{DB}. After reanalysis, it was determined that the points less than or equal to the inflection point had a linear slope equal to zero.

Addition of dew point

After mild, moderate, and severe HS thresholds were estimated for T_{DB}, DP was added to the model when significant to better fit the model. Dew point represents a true indication of the amount of moisture in the air [54], which was evaluated to determine best fit of the model. The DP inflection points for mild, moderate, and severe HS were determined and were calculated similarly to the T_{DB} inflection points. Based on the AIC and residual variance (Table 1), DP minus DP inflection point was used in the final model. When DP was not significant, DP was removed from the model completely (Table 1). Finally, the cross product of (T_{DB} – T_{DB} inflection point) × (DP – DP inflection point) was also added to the model, based on the improved AIC and residual variance.

Establishing cool, comfortable, and warm TDB thresholds

The behavioral thermal preference data used to establish cool, comfortable, and warm T_{DB} thresholds in this study were previously collected and published by our group [55]. All live animal data collection procedures were approved by the Purdue University Animal Care and Use Committee (protocol #1712001652). Animal care and use standards were based upon the *Guide for the Care and Use of Agricultural Animals in Research and Teaching* [41]. Briefly, non-pregnant (n=7), mid-gestation (n=5; 58.5±5.7 d pregnant), and late-gestation (n=6; 104.7±2.8 d pregnant) multiparous maternal line (Yorkshire × Landrace; parity 3.4±1.2) sows were selected for testing [55]. Sow thermal preferences were tested using two custom designed thermal gradient apparatuses (12.2 m × 1.52 m × 1.86 m; L × W × H). The thermal gradient apparatuses provided a thermal gradient ranging from 10.35 ± 0.42 °C to 30.49 ± 0.45 °C that was

monitored using data loggers (HOBO Data Logger; U12-012, Onset Computer Corporation, MA, USA; temperature range of $-20\text{ }^{\circ}\text{C}$ to $70\text{ }^{\circ}\text{C}$ with accuracy of $\pm 0.35\text{ }^{\circ}\text{C}$ and RH range 5% to 95% with accuracy of $\pm 2.5\%$ to max 3.5%) placed 0.94 m above the floor and 0.61 m apart [55]. All sows were allowed a 24-h acclimation period within the thermal gradient apparatuses before being tested for an additional 24 h [55]. All sows were allowed to consume their entire daily diet ration (1.82 kg/d) immediately prior to entering the apparatuses per common commercial swine production practices [43] and no reproductive stage-related feed intake differences were observed as previously described [55]. Water was provided ad libitum within the thermal gradient apparatuses. While being housed within the thermal gradient apparatuses, sows were continuously videorecorded and sow location within the apparatuses was compared against T_{DB} measured by the closest data logger [55]. These data were used to generate cubic curves to determine peak T_{DB} preference and the thermal preference range for each reproductive stage [55]. In the present study, thermal preference data generated by Robbins et al. [55] were used to estimate the T_{DB} that non-pregnant, mid-gestation, and late-gestation sows found to be cool ($T_{DB} < T_{DB}$ preference range), comfortable ($T_{DB} = T_{DB}$ preference range), and warm (T_{DB} preference range $< T_{DB} <$ mild HS).

Results and discussion

Heat stress has well-documented negative effects on the health, productivity, and welfare of sows [31, 56, 57] and their future offspring [3, 14, 58]. As such, a variety of cooling methods have been developed and used in swine facilities to alleviate HS (i.e., floor cooling pads, evaporative cooling pads, chilled drinking water) [10, 59–61]. However, despite the availability and continued development of cooling and management strategies to mitigate HS, recommended or perceived temperature thresholds for implementation may not accurately reflect the thermal requirements of swine. For example, the most recent thermal recommendations for swine by the Federation of Animal Science Societies [41] are based upon 25- to 41-year-old data and likely do not accurately reflect the thermal requirements of swine with current genetics that have been selected for greater litter sizes, lean gain, and have overall greater metabolic heat production [9]. Additionally, these recommendations [26] do not differentiate by sow reproductive stage, which is important because HS sensitivity becomes greater as gestation advances [31, 62, 63]. Although some efforts have been made to develop thermal indices and thresholds for pigs, these efforts have largely focused on the use of theoretical predictions [36–39, 64], have had limited data collection in a relatively small number of non-pregnant sows [40], or

have attempted to apply indices originally developed for cattle to pigs [65], and none to our knowledge have differentiated by reproductive stage or used behavioral metrics of thermal preference to identify comfortable temperature ranges for pigs. Therefore, our overall goal was to develop a swine specific decision support tool using both behavioral and thermoregulatory metrics derived from animal experimentation that would provide thermal recommendations for sows at three reproductive stages.

As environmental temperatures begin to rise, cutaneous blood flow increases in an attempt by the body to dissipate excess metabolic heat from the core to the skin where it can be lost to the environment by conductive, convective, evaporative, and radiant heat loss mechanisms [2, 66]. As a result, T_S increases as heat gain from the environment becomes greater, and T_S has frequently been used as a non-invasive indicator of HS in pigs via the use of thermal imaging cameras [31, 67–69], infrared thermometers [23, 70], and thermocouple probes [71]. Therefore, the relationship between T_S and T_{DB} was assessed in the present study to determine whether it could be used as an accurate predictor of thermal stress. However, it was determined that T_S had a linear relationship with T_{DB} (Fig. 1) indicating that the increasing environmental heat load (as well as other factors such as air speed) was likely responsible for elevated T_S as opposed to the sows' biological response to HS and total physiological heat load. This observation has implications towards the use of thermal imaging to assess physiological HS in swine. The linear relationship between T_S and T_{DB} suggests that thermal imaging and other technologies that assess heat load based upon T_S may be useful for determining how T_S is directly affected by the environment and is consistent with earlier observations in other species [13]. However, these technologies may not be an accurate or precise method of determining total physiological heat load of an individual pig to assess physiological HS. Therefore, based on these data, T_S should be used in conjunction with other well-described metrics of HS assessment (i.e., RR, core body temperature, feed intake, etc.) [2, 60].

Evaporative heat loss via increased RR is an important method of thermoregulation for pigs as they do not possess functional sweat glands and must rely solely on heat loss through behavioral thermoregulation (i.e., wallowing, reduced feed intake, etc.) or via the skin and respiratory tract [2, 60, 72, 73]. Greater RR is often the first visual sign that pigs are suffering from HS and is considered an active form of heat loss by the sow and other species [13, 51, 52]. In the present study, the RR response to increasing T_{DB} at each reproductive stage was best described by cubic equations that differed by reproductive stage ($P < 0.05$; Table 1) and were used to calculate

the RR inflection points (Fig. 2). The RR inflection point was considered the primary thermoregulatory indicator of mild HS as described in the mild HS equations (Table 4) and decision support tool (Fig. 5). The inflection points at which RR increased in response to increasing T_{DB} for non-pregnant, mid-gestation, and late-gestation sows were 25.5, 25.1, and 24.0 °C, respectively (Fig. 2). Although these data confirm previous reports that RR increases at lower T_{DB} in late-gestation versus mid-gestation and non-pregnant sows [31], they contradict previously calculated RR thresholds with increasing T_{DB} . For example, when comparing RR to increasing T_{DB} in finisher pigs using a broken line assumption model, Huynh et al. [74] determined that the inflection point was 22 °C. It is important to note however that the finisher pigs in

the aforementioned study [74] were fed ad libitum (as opposed to maintenance feeding common in non-pregnant and gestating sows) [43], likely increasing their metabolic heat production and resulting in greater thermal sensitivity to rising T_{DB} . Furthermore, a recent review of 28 studies [75] reported an overall RR inflection point of 20 °C for pigs in response to increasing T_{DB} . However, in this report [75], data were combined from prepubertal gilts, gestating sows, farrowing sows, lactating sows, and dry, non-pregnant sows to generate this value. Furthermore, no differentiation by production stage or physiological state (i.e., lactating sows are more HS sensitive than gestating and non-pregnant sows) was considered, which would likely result in an imprecise RR threshold estimation given the well-described thermoregulatory

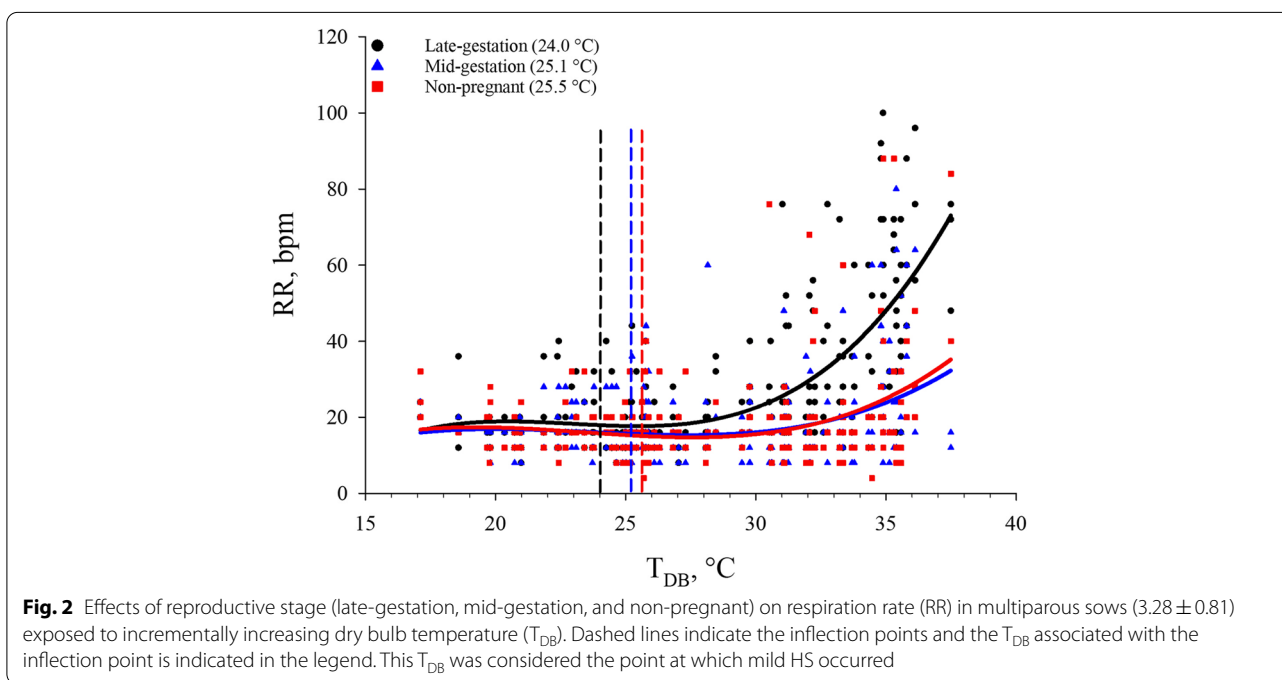


Fig. 2 Effects of reproductive stage (late-gestation, mid-gestation, and non-pregnant) on respiration rate (RR) in multiparous sows (3.28 ± 0.81) exposed to incrementally increasing dry bulb temperature (T_{DB}). Dashed lines indicate the inflection points and the T_{DB} associated with the inflection point is indicated in the legend. This T_{DB} was considered the point at which mild HS occurred

Table 4 Heat stress threshold equations to predict mild, moderate and severe heat stress in non-pregnant, mid-gestation, and late-gestation multiparous sows

| Reproductive phase | Heat stress category | Equations |
|--------------------|----------------------|--|
| Non-pregnant | Mild | $RR = 14.9527 + (-0.2009)(T_{DB} - 25.5) + (0.07377)(T_{DB} - 25.5)^2 + (0.005744)(T_{DB} - 25.5)^3$ |
| | Moderate and severe | $T_B = 38.1414 + (0.03256)(T_{DB} - 28.1) + (0.003542)(T_{DB} - 28.1)^2 + (0.000264)(T_{DB} - 28.1)^3$ |
| Mid-gestation | Mild | $RR = 18.8330 + (0.1373)(T_{DB} - 25.1) + (-0.00238)(T_{DB} - 25.1)^2 + (0.006759)(T_{DB} - 25.1)^3 + (0.2227)(DP - 22.2) + (0.03973)(T_{DB} - 25.1)(DP - 22.2)$ |
| | Moderate and severe | $T_B = 38.1325 + (0.05510)(T_{DB} - 27.8) + (0.001667)(T_{DB} - 27.8)^2 + (0.001163)(DP - 18.0) + (0.002696)(T_{DB} - 27.8)(DP - 18.0)$ |
| Late-gestation | Mild | $RR = 18.8849 + (0.02073)(T_{DB} - 24.0) + (0.02126)(T_{DB} - 24.0)^2 + (0.02018)(T_{DB} - 24.0)^3 + (0.1000)(DP - 19.1) + (0.02331)(T_{DB} - 24.0)(DP - 19.1)$ |
| | Moderate and severe | $T_B = 38.1860 + (0.03922)(T_{DB} - 25.5) + (-0.00181)(T_{DB} - 25.5)^2 + (0.000201)(T_{DB} - 25.5)^3 + (0.01115)(DP - 17.8)$ |

RR Respiration rate, T_{DB} Dry bulb temperature, T_B Body temperature, DP Dew point

differences that exist by reproductive and production stage [29–31].

When heat gain from the environment overwhelms sensible and latent heat loss mechanisms, T_B will begin to rise above the euthermic T_B in response to increasing T_{DB} [13]. In the present study, it was determined that the T_B inflection point was best described by cubic equations that differed by reproductive stage ($P < 0.05$; Table 1). Body temperature inflection points for non-pregnant, mid-gestation, and late-gestation sows occurred at 0.10 °C above euthermic T_B and at a T_{DB} of 28.1, 27.8, and 25.5 °C, respectively (Fig. 3). The T_B inflection points for non-pregnant, mid-gestation, and late-gestation sows were used as the primary thermoregulatory indicator in the moderate HS equations (Table 4) and in the decision support tool (Fig. 5). This decrease in T_B inflection point with advancing reproductive stage was expected when considering the previously described increase in HS sensitivity as gestation advances [29–31, 34]. To our knowledge, this is the first study to describe the T_{DB} threshold at which heat loss mechanisms fail to allow sows at three reproductive stages with current genetics to maintain a euthermic T_B . Although these T_{DB} inflection points cannot be considered the upper critical temperature (e.g., the point at which T_B begins to rise uncontrollably) [13], these data may provide a more precise T_{DB} threshold by which HS mitigation strategies should be employed in commercial swine facilities. Furthermore, it should be noted that the T_B inflection points at all reproductive stages were 3.9 to 6.5 °C less than what is currently

described as the upper temperature extreme for sows > 100 kg (32 °C) [26].

An abrupt and uncontrolled T_B increase occurs when the upper critical temperature limit (UCT) has been reached [13]. In the present study, it was determined that the T_{DB} threshold at which the abrupt T_B increase occurred was at 0.20 °C above euthermic T_B , and that it was similar ($P > 0.05$; 32.9 °C) for non-pregnant and mid-gestation sows, and lower ($P < 0.05$; 30.8 °C) for late-gestation versus non-pregnant and mid-gestation sows (Fig. 4). The T_B inflection points at which the abrupt T_B increase (0.20 °C) occurred for non-pregnant, mid-gestation, and late-gestation sows were used as the primary thermoregulatory indicator in the severe HS equations (Table 4) and in the decision support tool (Fig. 5). As expected, the severe HS threshold (e.g., the UCT) for late-gestation sows was deemed to be 1.2 °C lower than current guidelines for sows > 100 kg (32 °C) [26], and this response indicated that current UCT guidelines may not accurately reflect the severe HS threshold of late-gestation sows, which have greater heat gain and HS sensitivity when compared to non-pregnant and mid-gestation sows likely due to fetal growth [31]. However, the UCT for non-pregnant and mid-gestation sows in the present study was 0.90 °C greater than current > 100 kg sow guidelines (32 °C) [26]. While this response was unexpected given the aforementioned genetic advancements that have increased swine metabolic heat production [9, 76, 77] and likely sensitivity, this response may be explained by feed intake differences related to metabolic heat production and heat gain. In the

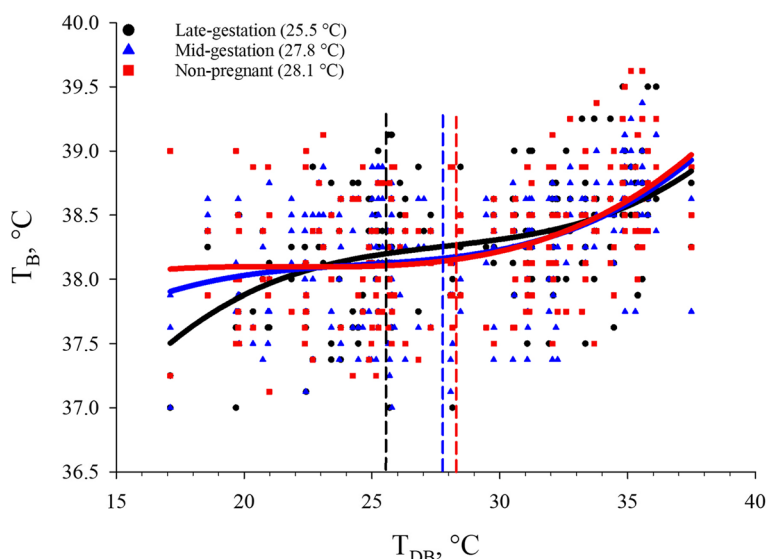


Fig. 3 Effects of reproductive stage (late-gestation, mid-gestation, and non-pregnant) on body temperature (T_B) in multiparous (3.28 ± 0.81) sows exposed to incrementally increasing dry bulb temperature (T_{DB}). Dashed lines indicate the inflection points and the T_{DB} associated with the inflection point is indicated in the legend. This T_{DB} was considered the point at which moderate HS occurred

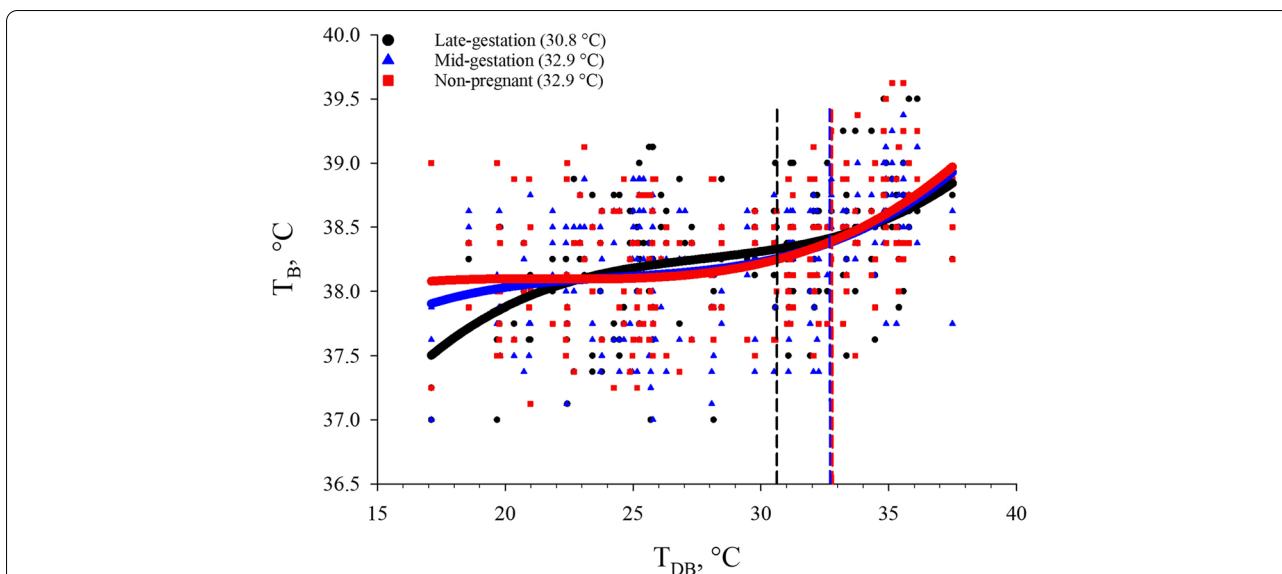


Fig. 4 Effects of reproductive stage (late-gestation, mid-gestation, and non-pregnant) on body temperature (T_B) in multiparous (3.28 ± 0.81) sows exposed to incrementally increasing dry bulb temperature (T_{DB}). Dashed lines indicate the point at which T_B increased abruptly ($+0.20$ °C) above baseline T_B and the T_{DB} associated with this point is indicated in the legend. This T_{DB} was considered the point at which severe HS occurred

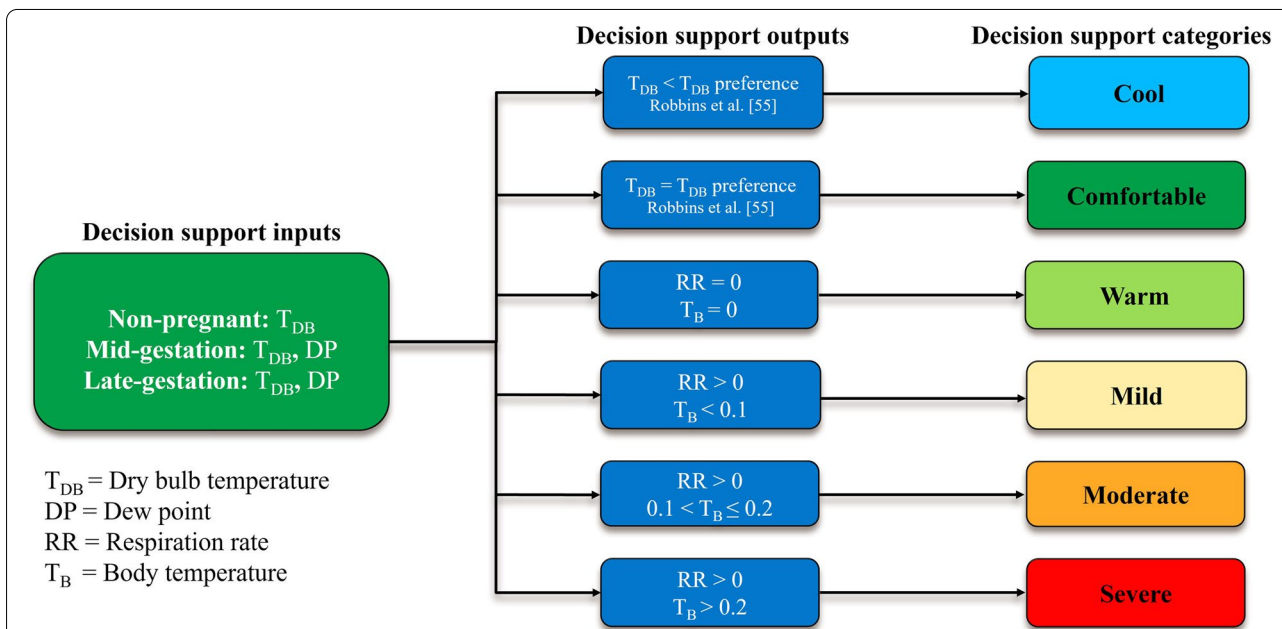


Fig. 5 A behavior and physiology-based decision support tool designed to predict thermal comfort and stress in non-pregnant, mid-gestation, and late-gestation sows

present study and in commercial practice, gestating sows and non-pregnant sows in the breeding population are fed at maintenance to prevent excessive maternal weight gain [43]. This would likely lead to a decrease in heat production when compared to ad libitum fed populations as increased feed intake is associated with greater heat

production due to the heat increment of feeding [13, 78]. Therefore, because current guidelines [26] do not differentiate by production stage, physiological state, or feeding level, it is likely that the UCT may be slightly greater for limit-fed sows > 100 kg based upon results from the present study (Fig. 4).

Relative humidity may play a role in the thermoregulatory response of pigs, particularly at greater T_{DB} [74]. For example, the efficacy of respiratory heat exchange with the environment is influenced by RH, and greater RH during HS causes increased RR in pigs [79]. In addition, increasing RH at greater T_{DB} leads to reductions in average daily body weight gain in grow-finish pigs [74]. As such, in addition to T_{DB} , DP was incorporated in the development of the HS threshold equations (Table 4) for use in the decision support tool (Fig. 5). However, it was determined that the addition of DP was only significant ($P < 0.05$) for mid- and late-gestation sows and did not influence the RR or T_B response of non-pregnant sows (Table 1). This lack of a significant response to DP ($P > 0.05$) by non-pregnant sows may be due to their reduced HS sensitivity relative to mid- and late-gestation sows as we have previously reported [31]. Therefore, this may result in a decreased requirement for the activation of heat loss mechanisms and likely a reduced RR and T_B sensitivity to adverse climactic conditions in non-pregnant sows fed at maintenance.

Many thermal indices have used animal-based thermoregulatory responses to quantify HS intensity and often consider any T_{DB} below the HS threshold to be the T_{DB} range at which the species of interest is comfortable [80]. However, the absence of an active thermoregulatory (e.g., increased RR and T_S) or T_B response is not necessarily an indicator of thermal comfort. This is because the transition from the thermal comfort zone to the warm zone is defined by limited thermoregulatory reactions defined by passive facilitation of heat loss that will intensify as T_{DB} increases [13]. As long as heat gain is balanced with heat loss, the animal is considered to be at thermoneutrality [81]; however, this T_{DB} range may not be reflective of an animal's thermal comfort zone (e.g., the T_{DB} range in which an individual prefers to spend time in and feels relaxed) [80]. As such, the thermal preferences of non-pregnant, mid-gestation, and late-gestation sows were incorporated into the decision support tool (Fig. 5), and data were derived from a previous report by our group [55]. These data [55] indicate that non-pregnant and mid-gestation animals prefer a similar ($P > 0.05$) T_{DB} range (13.2 to 16.4 °C) while late-gestation sows prefer a slightly lower ($P < 0.05$) T_{DB} range (12.6 to 15.6 °C). Therefore, for utilization in the decision support tool (Fig. 5), the thermal comfort zone was defined as the T_{DB} range in which the sows prefer to spend most of their time. Additionally, based upon the thermal preference data, the cool zone was defined as any T_{DB} below the lower limit of the thermal comfort zone, and the warm zone was defined as the T_{DB} range

in-between the upper limit of the thermal comfort zone and the start of mild HS (Fig. 2). Although maintaining facilities at sows' thermal comfort zone may not be feasible during hotter times of the year or in regions with prolonged periods of HS, these guidelines may be useful during cooler times of the year when determining facility heating requirements.

Conclusions

This study established HS thresholds and developed equations to predict mild, moderate, and severe HS in commercially relevant non-pregnant, mid-gestation, and late-gestation sows. These data were combined with thermal preference data previously reported by our group to develop a behavior and physiology-based decision support tool to predict thermal comfort and HS. Based on results from the present study, HS thresholds were influenced by reproductive stage and differed from previously established thresholds. In addition, the decision support tool developed through this research may be used to predict environmental conditions sows consider to be cool, comfortable, warm, mild HS, moderate HS, and severe HS. To our knowledge, this is the first thermal index developed specifically for gestating sows that incorporates both physiological and behavioral metrics of thermal preference and stress.

Abbreviations

AIC: Akaike's Information Criteria; B_0 : Intercept; B_1 : Linear regression coefficient; DP: Dew point; HS: Heat stress; IUHS: In utero heat stress; RH: Relative humidity; RR: Respiration rate; T_B : Body temperature; T_{DB} : Dry bulb temperature; THI: Thermal humidity index; TN: Thermoneutral; T_S : Skin temperature.

Acknowledgements

We would like to thank the Purdue University Swine Farm staff and students as well as the USDA-ARS Livestock Behavior Research Unit employees for their help with data collection, animal care, and lab analyses.

Authors' contributions

JSJ, BRM, and APS conceived and designed the experiment. JSJ, BRM, LR, BNG, ARG, and DCL completed the live animal trials. BRM and APS conducted statistical analyses. JSJ, BRM, LR, BNG, ARG, and DCL contributed to interpretation of results. JSJ, BRM, and APS wrote the manuscript. All authors read and approved the final version of the manuscript.

Funding

This research was supported by the USDA National Institute of Food and Agriculture – Agriculture and Food Research Initiative (grant no. 2018–67015-28130). In addition, this research was supported by an appointment to the Agricultural Research Service (ARS) Research Participation Program administered by the Oak Ridge Institute for Science and Education (ORISE) through an interagency agreement between the U.S. Department of Energy (DOE) and the U.S. Department of Agriculture (USDA). ORISE is managed by ORAU under DOE contract number DE-SC0014664.

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request. All statistical codes used to analyze data are available as supplementary files.

Declarations

Ethics approval and consent to participate

All live animal data collection procedures were approved by the Purdue University Animal Care and Use Committee (protocol ##1712001652 and #1811001823).

Consent for publication

Not applicable.

Competing interests

The authors declare they have no competing interests. Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture. All opinions expressed in this paper are the author's and do not necessarily reflect the policies and views of USDA, ARS, DOE, or ORAU/ORISE.

Author details

¹Oak Ridge Institute for Science and Education, Oak Ridge, TN 37830, USA. ²Department of Animal Sciences, Purdue University, West Lafayette, IN 47907, USA. ³Department of Agricultural and Biological Engineering, University of Illinois, Urbana, IL 61801, USA. ⁴USDA-ARS Livestock Behavior Research Unit, West Lafayette, IN 47907, USA.

Received: 24 May 2022 Accepted: 3 October 2022

Published online: 10 December 2022

References

1. Johnson JS, Abuajamieh M, Sanz-Fernandez MV, Seibert JT, Stoakes SK, Neetba J, et al. Thermal stress alters post-absorptive metabolism during pre- and postnatal development. In: Sejian V, Gaughan J, Baumgard L, Prasad C, editors. *Climate change impact on livestock: adaptation and mitigation*. New Delhi: Springer; 2015. p. 61–79.
2. Johnson JS. Evaluating and mitigating the impact of heat stress on livestock well-being and productivity. *Anim Prod Sci*. 2018;58:1404–13. <https://doi.org/10.1071/AN17725>.
3. Johnson JS, Stewart KR, Safranski TJ, Ross JW, Baumgard LH. In utero heat stress alters postnatal phenotypes in swine. *Theriogenology*. 2020;154:110–1. <https://doi.org/10.1016/j.theriogenology.2020.05.013>.
4. Lindsey R, Dahlgren L. Climate change: Global temperature. National Oceanic and Atmospheric Administration. 2020. <https://www.climate.gov/newsfeatures/understandingclimate/climate-change-global-temperature>. Accessed 17 March 2020.
5. NOAA National Centers for Environmental Information. State of the Climate: National Climate Report. 2019. <https://www.ncdc.noaa.gov/sotc/national/202001>. Assessed 21 March 2020.
6. Solá-Oriol D, Gasa J. Feeding strategies in pig production: Sows and their piglets. *Anim Feed Sci Technol*. 2017;233:34–52. <https://doi.org/10.1016/j.anifeeds.2016.07.018>.
7. Strathe AV, Bruun TS, Hansen CF. Sows with high milk production had both a high feed intake and high body mobilization. *Anim*. 2017;11:1913–21. <https://doi.org/10.1017/S1751731117000155>.
8. Wu Y, Zhao C, Xu C, Ma N, He T, Zhao J, et al. Progress towards pig nutrition in the last 27 years. *Sci Food Agric*. 2018;100:5102–10. <https://doi.org/10.1002/jsfa.9095>.
9. Stinn JP, Xin H. Heat and moisture production rates of a modern US swine breeding, gestation, and farrowing facility. *Trans ASABE*. 2014;57:1517–28. <https://doi.org/10.13031/trans.57.10711>.
10. Cabezon FA, Schinckel AP, Smith AJ, Marchant-Forde JN, Johnson JS, Stwalley RM. Initial evaluation of floor cooling on lactating sows under acute heat stress. *Prof Anim Sci*. 2017;33:254–60. <https://doi.org/10.15232/pas.2017-01661>.
11. Johnson JS, Zhang S, Morello GM, Maskal JM, Trottier NL. Development of an indirect calorimetry system to determine heat production in individual lactating sows. *J Anim Sci*. 2019;97:1609–18. <https://doi.org/10.1093/jas/skz049>.

12. Noblet J, Etienne M. Metabolic utilization of energy and maintenance requirements in pregnant sows. *Livest Prod Sci*. 1987;68:562–72. [https://doi.org/10.1016/0301-6226\(87\)90042-X](https://doi.org/10.1016/0301-6226(87)90042-X).
13. Curtis SE. *Environmental management in animal agriculture*. Ames, Iowa: Iowa State University Press; 1983. p. 6–96.
14. Johnson JS, Baumgard LH. Physiology Symposium: Postnatal consequences of prenatal heat stress in pigs. *J Anim Sci*. 2019;97:962–71. <https://doi.org/10.1093/jas/sky472>.
15. Johnson JS, Sanz Fernandez MV, Patience JF, Ross JW, Gabler NK, Lucy MC, et al. Effects of in utero heat stress on postnatal body composition in pigs: II. Finishing phase. *J Anim Sci*. 2015;93:82–92. <https://doi.org/10.2527/jas.2014-8355>.
16. Maskal JM, Duttlinger AW, Kpodo KR, McConn BR, Byrd CJ, Richert BT, et al. Evaluation and mitigation of the effects of in utero heat stress on piglet growth performance, postabsorptive metabolism, and stress response following weaning and transport. *J Anim Sci*. 2020;98:skaa265. <https://doi.org/10.1093/jas/skaa265>.
17. Byrd CJ, Anderson NC, Lugar DW, Safranski TJ, Lucy MC, Johnson JS. Evaluating the effects of in utero heat stress on piglet physiology and behavior following weaning and transport. *Animals (Basel)*. 2019;9:191. <https://doi.org/10.3390/ani9040191>.
18. Merlot E, Constancis C, Resmond R, Serviento AM, Renaudeau D, Prunier A, et al. Heat exposure of pregnant sows modulates behaviour and corticosterone axis responsiveness of their offspring after weaning. In: *Proceedings of the 53rd Congress of the International Society for Applied Ethology*. Bergen, Norway: Wageningen Academic Publishers; 2019.
19. Machado-Neto R, Graves CN, Curtis SE. Immunoglobulins in piglets from sows heat stressed prepartum. *J Anim Sci*. 1987;65:445–55. <https://doi.org/10.2527/jas1987.652445x>.
20. Chapel NM, Byrd CJ, Lugar DW, Morello GM, Baumgard LH, Ross JW, et al. Determining the effects of early gestation in utero heat stress on postnatal fasting heat production and circulating biomarkers associated with metabolism in growing pigs. *J Anim Sci*. 2017;95:3914–21. <https://doi.org/10.2527/jas2017.1730>.
21. Guo H, He J, Yang X, Zheng W, Yao W. Responses of intestinal morphology and function in offspring to heat stress in primiparous sows during late gestation. *J Therm Biol*. 2020;89:102539. <https://doi.org/10.1016/j.jtherbio.2020.102539>.
22. Johnson JS, Boddicker RL, Sanz-Fernandez MV, Ross JW, Selsby JT, Lucy MC, et al. Effects of mammalian in utero heat stress on adolescent body temperature. *Int J Hyperthermia*. 2013;29:696–702. <https://doi.org/10.3109/02656736.2013.843723>.
23. Johnson JS, Sanz Fernandez MV, Seibert JT, Ross JW, Lucy MC, Safranski TJ, et al. In utero heat stress increases postnatal core body temperature in pigs. *J Anim Sci*. 2015;93:4312–22. <https://doi.org/10.2527/jas2015-9112>.
24. Lugar DW, Proctor JA, Safranski TJ, Lucy MC, Stewart KR. In utero heat stress causes reduced testicular area at puberty, reduced total sperm production, and increased sperm abnormalities in boars. *Anim Reprod Sci*. 2018;192:126–35. <https://doi.org/10.1016/j.anireprosci.2018.02.022>.
25. Johnson JS, Maskal JM, Duttlinger AW, Kpodo KR, McConn BR, Byrd CJ, et al. In utero heat stress alters the postnatal innate immune response of pigs. *J Anim Sci*. 2020;98:1–13. <https://doi.org/10.1093/jas/skaa356>.
26. Hill G, Lay Jr DC, Radcliffe S, Richert B. Chapter 9: swine. In: Tucker CB, MacNeil MD, Webster AB, editors. *Guide for the care and use of agricultural animals in research and teaching*. Champaign, IL: American Dairy Science Association, American Society of Animal Science, Poultry Science Association; 4th ed; 2020. p. 127–140.
27. Holmes CW, Close WH. The influence of climatic variables on energy metabolism and associated aspects of productivity in the pig. In: *Nutrition and the climatic environment of pigs*. London: Butterworths; 1977. p. 51–73.
28. Hahn GL. Managing and housing of farm animals in hot environments in stress physiology in livestock. In: Yousef MK, editor. *Stress physiology in livestock vol II: ungulates*. Boca Raton, Florida: CRC Press; 1985. p. 151–74.
29. Heitman H, Hughes EH, Kelly CF. Effects of elevated ambient temperature on pregnant sows. *J Anim Sci*. 1951;10:907–15. <https://doi.org/10.2527/jas1951.104907x>.
30. Omtvedt IT, Nelson RE, Edwards RL, Stephens DF, Turman EJ. Influence of heat stress during early, mid and late pregnancy of gilts. *J Anim Sci*. 1971;32:312–7. <https://doi.org/10.2527/jas1971.322312x>.

31. McCann BR, Gaskill BN, Schinckel AP, Green-Miller AR, Lay Jr DC, Johnson JS. Thermoregulatory and physiological responses of nonpregnant, mid-gestation, and late-gestation sows exposed to incrementally increasing dry bulb temperature. *J Anim Sci*. 2021;99:skab181. <https://doi.org/10.1093/jas/skab181>.
32. National Weather Service Central Region (NWSR). Livestock hot weather stress. Regional operations manual letter C-31–76. US Dept. Commerce, Natl. Oceanic and Atmospheric Admin. 1976.
33. Zumbach B, Misztal I, Tsuruta S, Sanchez JP, Azain M, Herring W, et al. Genetic components of heat stress in finishing pigs: parameter estimation. *J Anim Sci*. 2008;86:2076–81. <https://doi.org/10.2527/jas.2007-0282>.
34. Zumbach B, Misztal I, Tsuruta S, Sanchez JP, Azain M, Herring W, et al. Genetic components of heat stress in finishing pigs: development of a heat load function. *J Anim Sci*. 2008;86:2081–8. <https://doi.org/10.2527/jas.2007-0523>.
35. Usala M, Macciotta NPP, Bergamaschi M, Maltecca C, Fix J, Schwab C, et al. Genetic parameters for tolerance to heat stress in crossbred swine carcass traits. *Front Genet*. 2021;11:612815. <https://doi.org/10.3389/fgene.2020.612815>.
36. Ramirez BC. A novel approach to measure, understand, and assess the thermal environment in grow-finish swine facilities. Iowa State University; 2017. <https://doi.org/10.31274/etd-180810-5830>.
37. Huang T, Rong L, Zhang G, Brandt P, Bjerg B, Pedersen P, et al. A two-node mechanistic thermophysiological model for pigs reared in hot climates—Part 1: Physiological responses and model development. *Biosyst Eng*. 2021;212:302–17. <https://doi.org/10.1016/j.biosystemseng.2021.08.024>.
38. Cao M, Zong C, Wang X, Teng G, Zhuang Y, Lei K. Modeling of heat stress in sows—Part 1: Establishment of the prediction model for the equivalent temperature index of the sows. *Animals (Basel)*. 2021;11:1472. <https://doi.org/10.3390/ani11051472>.
39. Huang T, Rong L, Zhang G, Brandt P, Bjerg B, Pedersen P, et al. A two-node mechanistic thermophysiological model for pigs reared in hot climates—Part 2: Model performance assessments. *Biosyst Eng*. 2021;212:318–35. <https://doi.org/10.1016/j.biosystemseng.2021.08.021>.
40. Cao M, Zong C, Zhuang Y, Teng G, Zhou S, Yang T. Modeling of heat stress in sows—Part 2: Comparison of various comfort indices. *Animals (Basel)*. 2021;11:1498. <https://doi.org/10.3390/ani11061498>.
41. Federation of Animal Science Societies. Guide for the care and use of agricultural animals in research and teaching. 3rd ed. Fed Anim Sci Soc; 2010. chap 11.
42. Kpodo KR, Duttlinger AW, Radcliffe JS, Johnson JS. Time course determination of the effects of rapid and gradual cooling after acute hyperthermia on body temperature and intestinal integrity in pigs. *J Therm Biol*. 2020;87:102481. <https://doi.org/10.1016/j.jtherbio.2019.102481>.
43. National Research Council. Nutrient requirements of swine. Washington DC, USA: National Academy Press; 2012.
44. Akaike H. Information theory and an extension of the maximum likelihood principle. In: Parzen E, Tanabe K, Kitagawa G, editors. Selected papers of Hirotugu Akaike. Springer series in statistics. New York, NY: Springer; 1998. p. 199–213.
45. Akaike H. A new look at the statistical model identification. *IEEE Trans Automat Contr*. 1974;19:716–23. <https://doi.org/10.1109/TAC.1974.1100705>.
46. Burnham KP, Anderson DR. Multimodel inference: understanding AIC and BIC in model selection. *Sociol Methods Res*. 2004;33:261. <https://doi.org/10.1177/0049124104268644>.
47. Liddle AR. Information criteria for astrophysical model selection. *Mon Not R Astron Soc Lett*. 2007;377:L74–8. <https://doi.org/10.1111/j.1745-3933.2007.00306.x>.
48. Barnett AG, Koper N, Dobson AJ, Schmiegelow F, Manseau M. Using information criteria to select the correct variance–covariance structure for longitudinal data in ecology. *Methods Ecol and Evol*. 2010;1:15–24. <https://doi.org/10.1111/j.2041-210X.2009.00009.x>.
49. Burnham KP, Anderson DR. Information and likelihood theory: A basis for model selection and interference. In: Model selection and multimodel inference: A practical information-theoretic approach. 2nd ed. New York, NY: Springer-Verlag; 2002. p. 49–97.
50. Robbins KR, Saxton AM, Southern LL. Estimation of nutrient requirements using broken-line regression analysis. *J Anim Sci*. 2006;84:E155–65. <https://doi.org/10.2527/2006.8413suppl155x>.
51. Brown-Brandl TM, Nienaber JA, Turner LW. Acute heat stress effects on heat production and respiration rate in swine. *Trans ASAE*. 1998. <https://doi.org/10.13031/2013.17216>.
52. Brown-Brandl TM, Eigenberg RA, Nienaber JA, Kachman SD. Thermoregulatory profile of a newer genetic line of pigs. *Livest Prod Sci*. 2001;71:253–60. [https://doi.org/10.1016/S0301-6226\(01\)00184-1](https://doi.org/10.1016/S0301-6226(01)00184-1).
53. Baker JE. Effective environmental temperature. *J Swine Health Prod*. 2004;12:140–3.
54. Zulovich JM. Effect of the environment on health. In: Zimmerman JJ, Karriker LA, Ramirez A, Schwartz KJ, Stevenson GW, editors. Diseases of Swine. 10th ed. West Sussex, UK: John Wiley & Sons, Inc; 2012. p. 60–6.
55. Robbins LA, Green-Miller AR, Lay DC Jr, Schinckel AP, Johnson JS, Gaskill BN. Evaluation of sow thermal preference across three stages of reproduction. *J Anim Sci*. 2021. <https://doi.org/10.1093/jas/skab202>.
56. Muns R, Malmkvist J, Larsen MLV, Sørensen D, Pedersen LJ. High environmental temperature around farrowing induced heat stress in crated sows. *J Anim Sci*. 2016;94:377–84. <https://doi.org/10.2527/jas2015-9623>.
57. Kim SW, Weaver AC, Shen YB, Zhao Y. Improving efficiency of sow productivity: nutrition and health. *J Anim Sci Biotechnol*. 2013. <https://doi.org/10.1186/2049-1891-4-26>.
58. Lucy MC, Safranski TJ. Heat stress in pregnant sows: thermal responses and subsequent performance of sows and their offspring. *Molec Reprod Devel*. 2017. <https://doi.org/10.1002/mrd.22844>.
59. Jeon JH, Yeon SC, Choi YH, Min W, Kim S, Kim PJ, et al. Effects of drinking water on the performance of lactating sows and their litters during high ambient temperatures under farm conditions. *Livest Sci*. 2006;105:86–93. <https://doi.org/10.1016/j.livsci.2006.04.035>.
60. Mayorga EJ, Renaudeau D, Ramirez BC, Ross JW, Baumgard LH. Heat stress adaptations in pigs. *Anim Front*. 2019;9:54–61. <https://doi.org/10.1093/af/vfy035>.
61. Godyń D, Herbut P, Angrecka S, Vieira FMC. Use of different cooling methods in pig facilities to alleviate the effects of heat stress—a review. *Animals*. 2020. <https://doi.org/10.3390/ani10091459>.
62. King G, Willoughby RA, Hacker RR. Fluctuations in rectal temperature of swine at parturition. *Can Vet J*. 1972;13:72–4.
63. Hendrix WF, Kelley KW, Gaskins CT, Bendel RB. Changes in respiratory rate and rectal temperature of swine near parturition. *J Anim Sci*. 1978;47:188–91. <https://doi.org/10.2527/jas1978.471188x>.
64. Dourmad JY, Velly VL, Lechartier C, Gourdine JL, Renaudeau D. Effect of ambient temperature on lactating sows, a meta-analysis and modeling approach. *Journées de la Recherche Porcine en France*. 2015;47:105–10.
65. Hahn GL, Gaughan JB, Mader TL, Eigenberg RA. Chapter 5: Thermal indices and their applications for livestock environments. In: DeShazer JA, editor. Livestock energetics and thermal environmental management. St. Joseph, MI: American Society of Agricultural and Biological Engineers; 2009. p. 113–30.
66. Roberts MF, Wenger CB. Control of skin circulation during exercise and heat stress. *Med Sci Sports*. 1979;11:36–41.
67. Warriss PD, Pope SJ, Brown SN, Wilkins LJ, Knowles TG. Estimating the body temperature of groups of pigs by thermal imaging. *Vet Rec*. 2006;158:331–4. <https://doi.org/10.1136/vr.158.10.331>.
68. Brown-Brandl TM, Eigenberg RA, Purswell JL. Using thermal imaging as a method of investigating thermal thresholds in finishing pigs. *Biosyst Eng*. 2013;114:327–33. <https://doi.org/10.1016/j.biosystemseng.2012.11.015>.
69. Sapkota A, Herr A, Johnson JS, Lay DC. Core body temperature does not cool down with skin surface temperature during recovery at room temperature after acute heat stress exposure. *Livest Sci*. 2016;191:143–7. <https://doi.org/10.1016/j.livsci.2016.07.010>.
70. Johnson JS, Sapkota A, Lay DC Jr. Rapid cooling after acute hyperthermia alters intestinal morphology and increases the systemic inflammatory response in pigs. *J Appl Physiol*. 2016. <https://doi.org/10.1152/jappphysiol.00685.2015>.
71. Serviento AM, Lebreton B, Renaudeau D. Chronic prenatal heat stress alters growth, carcass composition, and physiological response of growing pigs subjected to postnatal heat stress. *J Anim Sci*. 2020. <https://doi.org/10.1093/jas/skaa161>.
72. Richards SA. The significance of changes in the temperature of the skin and body core of the chicken in the regulation of heat loss. *J Physiol*. 1971. <https://doi.org/10.1113/jphysiol.1971.sp009505>.

73. Ingram DL. Heat loss and its control in pigs. In: Monteith JL, Mount LE, editors. Heat loss from animals and man. London: Butterworths; 1973. p. 235–54.
74. Huynh TTT. Heat stress in growing pigs. PhD thesis. Wageningen Institute of Animal Science, Wageningen University: ProQuest; 2005.
75. Bjerg B, Brandt P, Pedersen P, Zhang G. Sows' responses to increased heat load—A review. *J Therm Biol*. 2020. <https://doi.org/10.1016/j.jtherbio.2020.102758>.
76. Brown-Brandl TM, Hayes MD, Xin H, Nienaber JA, Li H. Heat and moisture production of modern swine. *ASHRAE Trans*. 2014;120:469–89. <https://doi.org/10.13031/trans.57.1071>.
77. Ross JW, Hale BJ, Seibert JT, Romoser MR, Adur MK, Keating AF, et al. Physiological mechanisms through which heat stress compromises reproduction in pigs. *Mol Reprod Dev*. 2017. <https://doi.org/10.1002/mrd.22859>.
78. Noblet J, Shi XS, Dubois S. Energy cost of standing activity in sows. *Livest Prod Sci*. 1993;34:127–36. [https://doi.org/10.1016/0301-6226\(93\)90041-F](https://doi.org/10.1016/0301-6226(93)90041-F).
79. Heitman H Jr, Hughes EH. The effects of air temperature and relative humidity on the physiological well being of swine. *J Anim Sci*. 1949;8:171–81. <https://doi.org/10.2527/jas1949.82171x>.
80. Kingma B, Frijns A, van Marken LW. The thermoneutral zone: implications for metabolic studies. *Front Biosci*. 2012;4:1975–85.
81. IUPS Thermal Commission revised. Glossary of terms for thermal physiology. 3rd ed. *Japanese J Physiol*. 2001;51:245–80.

Ready to submit your research? Choose BMC and benefit from:

- fast, convenient online submission
- thorough peer review by experienced researchers in your field
- rapid publication on acceptance
- support for research data, including large and complex data types
- gold Open Access which fosters wider collaboration and increased citations
- maximum visibility for your research: over 100M website views per year

At BMC, research is always in progress.

Learn more biomedcentral.com/submissions

