Characterizing the acute heat stress response in gilts: I. Thermoregulatory and production variables

J. T. Seibert, K. L. Graves, B. J. Hale, A. F. Keating, L. H. Baumgard, and J. W. Ross¹

Department of Animal Science, Iowa State University, Ames, IA 50011

ABSTRACT: Identifying traits associated with susceptibility or tolerance to heat stress (HS) is a prerequisite for developing strategies to improve efficient pork production during the summer months. Study objectives were to determine the relationship between the thermoregulatory and production responses to acute HS in pigs. Prepubertal gilts ($n = 235$; 77.9 ± 1.2 kg BW) were exposed to a thermoneutral (TN) period (P1, 24 h; 21.9 ± 0.5 °C, $62 \pm 13\%$ RH; fed ad libitum) followed immediately by a subsequent acute HS period (P2, 24 h; 29.7 ± 1.3 °C, $49 \pm 8\%$ RH; fed ad libitum). Rectal temperature (T_R), skin temperature (T_S), and respiration rate (RR) were monitored and BW and feed intake (FI) were determined. All pigs had increased T_R , T_S , and RR (0.80 °C, 5.65 °C, and 61.2 bpm, respectively; $P < 0.01$) and decreased FI and BW (29% and 1.10 kg, respectively; $P < 0.01$) during P2 compared to P1. Interestingly, body temperature indices did not explain variation in FI during P2 ($R^2 \leq 0.02$). Further, the percent change

in BW during P2 was only marginally explained by each body temperature index ($R^2 \leq 0.06$) or percent change in FI ($R^2 = 0.14$). During HS, T_R was strongly correlated with P1 T_R ($r = 0.72$, $P < 0.01$), indicating a pig's body temperature during TN conditions predicts the severity of hyperthermia during HS. Additionally, the change in T_R (ΔT_R , HS $T_R -$ TN T_R) was larger in pigs retrospectively classified as susceptible (SUS) as compared to tolerant (TOL) pigs (1.05 vs. 0.51 °C, respectively; $P < 0.01$). In summary, thermoregulatory responses and production variables during acute HS are only marginally related. Further, changes in BW and FI were unexpectedly poorly correlated during acute HS ($r = 0.34$; $P < 0.01$). Collectively, suboptimal growth is largely independent on the thermoregulatory response and hypophagia during acute HS. Consequently, incorporating solely body temperature indices into a genetic index is likely insufficient for substantial progress in selecting HS tolerant pigs.

Key words: gilts, heat tolerance, thermoregulation

© The Author(s) 2018. Published by Oxford University Press on behalf of American Society of Animal Science. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com.

J. Anim. Sci. 2018.96:941–949

doi: 10.1093/jas/skx036

INTRODUCTION

Heat stress (HS) annually constrains pork profitability, independent of farm size and system. Lost economic opportunity primarily

results from increased mortality and morbidity, altered carcass composition, reduced fecundity, decreased and inconsistent growth, and compromised feed and facility efficiency (Baumgard and Rhoads, 2013). Porcine sweat glands are non-functional and the pig's thermoregulatory ability is further complicated by a thick subcutaneous adipose tissue layer, which impedes radiant heat loss (D'Allaire et al., 1996). Furthermore, genetic selection emphasizing rapid lean tissue accretion is accompanied by increased endogenous heat production; a thermal scenario that exacerbates their innate inability to tolerate heat (Bianca,

Results described here within were supported by the National Pork Board, the Iowa Pork Producers Association, and Agriculture and Food Research Initiative Competitive Grant no. 2011-67003-30007 from the USDA National Institute of Food and Agriculture.

¹Corresponding author: jwross@iastate.edu

Received September 8, 2017.

Accepted January 1, 2018.

1976; Renaudeau et al., 2011). Additionally, while HS is already a significant burden to the pig industry, production efficiency may be further compromised if climate patterns change as predicted (Intergovernmental Panel on Climate Change (IPCC), 2007; Hoffmann, 2010).

A conserved response to HS is reduced feed intake, ostensibly an attempt to minimize metabolic heat production (Bianca, 1976; Blaxter, 1989; Collin et al., 2001; Baumgard and Rhoads, 2013). Consequently, reduced feed intake has traditionally been assumed to be the major reason underlying negative effects of HS on production parameters in animal agriculture (Collin et al., 2001; West, 2003; DeShazer et al., 2009). However, utilizing a pair-feeding experimental design demonstrates that heat-induced hypophagia cannot fully explain the negative consequences of HS (Prunier et al., 1997; Baumgard and Rhoads, 2013; Pearce et al., 2013; Sanz Fernandez et al., 2015). Therefore, there are direct effects of HS (independent of reduced nutrient intake) that contribute to poor summer performance (Baumgard and Rhoads, 2013).

Incorporating a thermal sensitivity index into a genetic selection program that emphasizes HS tolerance without compromising other economically important traits would be valuable. However, identifying pigs that maintain productivity during HS, or that exhibit heat tolerance, is difficult due to the biological complexity of the HS response. Previous studies have shown “heat tolerance” with respect to minimizing the HS effects on a single production characteristic (Bloemhof et al., 2008; Zumbach et al., 2008). Thus, study objectives were to examine whether or not multiple thermoregulatory responses are associated with production phenotypes during acute HS. We hypothesized that animals retrospectively classified as tolerant (TOL) and susceptible (SUS) to HS based on their thermoregulatory response to an acute heat challenge would also have industry relevant productivity differences during HS.

MATERIALS AND METHODS

Animals and Experimental Design

All procedures were approved by the Iowa State University Institutional Animal Care and Use Committee. Crossbred gilts ($n = 235$; PIC maternal $\times$ Duroc terminal sire) from the same cohort were received at approximately 24 days of age immediately after weaning. Due to logistical constraints, the experiment was conducted in five replications

($n = 44$ to 48/replicate). The initial BW from replications 1 to 5 were 59 ± 1.0 , 64 ± 1.2 , 77 ± 1.2 , 88 ± 1.1 , and 103 ± 1.6 kg, respectively. Gilts were randomly assigned and housed in individual crates (57×221 cm; 24 crates/room) at the Iowa State University Swine Nutrition Farm research facility (Ames, IA). Each crate was equipped with a stainless steel feeder and a nipple drinker. Water and feed were provided ad libitum during the entire experiment.

All pigs were fed a standard diet consisting mainly of corn and soybean meal formulated to meet or exceed nutrient requirements (NRC, 2012; Supplementary Table 1). The study was divided into three experimental periods (P) for each replicate: P0, P1, and P2. Period 0 (72 h) served as an acclimation period in which all pigs were housed individually in thermoneutral (TN) conditions (21.9 ± 0.5 °C, $62 \pm 13\%$ relative humidity [RH]). After P0, pigs remained in TN conditions for 24 h (Period 1; P1) and then exposed to HS (29.7 ± 1.3 °C, $49 \pm 8\%$ RH) conditions for 24 h (Period 2; P2). Pigs were exposed to a 12:12 h light-dark cycle during P0, but continuous light during P1 and P2 to allow for accurate data collection.

Production and Thermoregulation Measurements

Rectal temperature (T_R) was measured with a calibrated and lubricated digital thermometer (Welch Allyn SureTemp Plus 690; accuracy: ± 0.1 °C; Skaneateles Falls, NY, USA), skin temperature (T_S) was measured using a calibrated infrared thermometer (HDE ST380A Infrared Thermometer; accuracy ± 2.0 °C, HDE, Allentown, PA), and respiration rate (RR) was determined by counting flank movements for 15 s and then multiplying by 4 to obtain breaths/min (bpm). Feed intake (FI) was measured daily and thermoregulatory indices were recorded for each pig hourly during both P1 and P2. Body weights were collected at the beginning of P0 and after P1 and P2. The percent change in BW ($\Delta BW\%$) and FI ($\Delta FI\%$) were calculated by subtracting each variable's P1 measurement from P2, dividing that value by the P1 measurement, and expressing the fraction as a percentage. Ambient temperature was controlled, but humidity was not governed and both parameters were recorded every 30 min by four data loggers (Lascar EL-USB-2-LCD, Erie, PA) in each room and later condensed into average values.

Determination of HS Tolerance and Susceptibility Based on the Thermoregulatory Response

All T_R data recorded hourly during P1 were condensed into an average value to represent each individual pig's basal core temperature (TN T_R). Only T_R data recorded hourly between the 4th and 12th h of HS were condensed into an average value to reflect core body temperature during P2 (HS T_R). These time points were chosen to minimize variability associated with both the rate of T_R increase (1 to 4 h) and the counter regulatory mechanisms (13 to 24 h) associated with T_R acclimation. The difference in core body temperature (ΔT_R) was calculated by subtracting TN T_R from the HS T_R . The ΔT_R was plotted against the HS T_R in order to determine the relationship between each pig's average HS T_R and ΔT_R . Since ΔT_R was highly associated with HS T_R ($r = 0.83$; $P < 0.01$; Table 2), each pig's tolerance to the heat load was classified solely on the basis of HS T_R (i.e., higher and lower HS T_R were considered reflective of HS susceptibility or tolerance, respectively). For each of the five replicates, the 10 most tolerant (TOL; $n = 50$) and susceptible (SUS; $n = 50$) pigs were identified (based only on HS T_R) and allocated to their retrospective classifications for statistical analysis.

Statistical Analysis

All data were statistically analyzed using SAS University Edition software, version 9.4 (SAS Institute Inc., Cary, NC). Thermoregulatory indices and production data were analyzed using PROC MIXED; the model included P and room as fixed effects, replication as a random effect, and the BW collected at the beginning of P0 as a covariate. To investigate relationships between variables, PROC CORR was used to generate Pearson's correlation coefficients. Thermoregulatory indices and production data associated with the retrospective TOL and SUS treatments were analyzed using PROC MIXED; the model included classification, P, and room as fixed effects, replication

as a random effect, and the BW collected at the beginning of P0 as a covariate. Data are reported as LSmeans and statistical significance ($P \leq 0.05$) and tendency ($0.05 < P \leq 0.10$) thresholds were utilized for interpretation of results.

RESULTS

Thermoregulatory and Productivity Variables have Marginal Relationships During TN Conditions

During P1, T_R , T_S , and RR were 39.03 ± 0.03 °C, 36.63 ± 0.07 °C, and 39.0 ± 0.8 bpm, respectively (Table 1). Period 1 FI was 2.48 ± 0.04 kg and BW was 84.4 ± 0.7 kg. A marginal association was observed for TN FI and TN T_R for all pigs in the study ($r = 0.03$; $P = 0.64$; Supplementary Table 2). Thermoneutral FI and ADG were correlated to each other ($r = 0.45$; $P < 0.01$; Supplementary Table 2), but TN T_R and ADG were poorly associated ($R^2 = 0.04$).

Minor Relationships Between Thermoregulation and Production Parameters Are Observed During HS Conditions

As expected, T_R , T_S , and RR were increased (0.80 °C, 5.65 °C, and 61.2 bpm, respectively; $P < 0.01$) during P2 compared to P1 (Table 1). The variation in each thermoregulatory parameter also increased during HS as the SD of T_R , T_S , and RR was increased during P2 compared to P1 (78%, 21%, and 197%, respectively; Fig. 1). Decreased FI (0.71 kg; $P < 0.01$; Table 1) and BW (1.09 kg; $P < 0.01$; Table 1) occurred during P2 relative to P1. During P2, $\Delta FI\%$ and T_R were weakly correlated ($r = -0.16$; $P = 0.03$; Supplementary Table 2 and Fig. 2A). Additionally, the heat-induced $\Delta BW\%$ was poorly associated with HS T_R ($r = -0.23$; $P < 0.01$; Supplementary Table 2 and Fig. 2B). Predictably, a general trend of increasing T_S ($r = 0.29$; $P < 0.01$; Supplementary Table 2 and Fig. 3A) or RR ($r = 0.35$;

Table 1. Effects of environment on thermoregulatory indices and production variables in growing pigs

Parameter	Period 1 ¹	Period 2 ²	SEM	P
Rectal temperature, °C	39.03	39.83	0.03	<0.01
Skin temperature, °C	36.63	42.27	0.11	<0.01
Respiration rate, bpm ³	39.0	100.2	1.8	<0.01
Feed intake, kg	2.48	1.77	0.06	<0.01
BW	84.4	83.3	0.7	<0.01

¹Thermoneutral (TN) conditions ²Heat stress (HS) conditions ³Breaths per minute

Figure 1. Box and whisker plots of rectal temperature (T_R ; A), skin temperature (T_S ; B), and respiration rate (RR; breaths per minute [bpm]; C) distributions during period (P) 1 (24-h thermoneutral [TN] conditions) and subsequently P2 (24-h heat stress [HS]). Considerable variation exists between animals with respect to their thermoregulatory response during HS as compared to TN conditions. Whiskers denote the minimum and maximum value for each P. The bottom and top boundaries of each box represents the first and third quartiles, respectively, while the inner middle line marks the median during each P.

$P < 0.01$; Supplementary Table 2 and Fig. 3B) with increasing T_R was observed during P2. During P2, RR and T_S were also correlated ($r = 0.23$; $P < 0.01$; Supplementary Table 2).

Relationship Between Thermoregulatory Indices and Production Characteristics During TN and HS Conditions

Interestingly, HS T_R was strongly correlated to TN T_R ($r = 0.72$; $P < 0.01$; Supplementary Table 2 and Fig. 4A). In addition, ΔT_R was correlated with TN T_R ($r = 0.21$; $P < 0.01$; Supplementary Table 2

Figure 2. Relationships between rectal temperature (T_R) and the change (Δ) in feed intake (FI) of pigs during period (P) 2 (heat stress [HS] conditions; A) and of HS T_R with the ΔBW (B). The ΔFI and ΔBW variables were determined by subtracting the P2 measurement from P1 (thermoneutral [TN] conditions).

and Fig. 4B). During HS, a low proportion of variation in $\Delta BW\%$ was explained by the $\Delta FI\%$ ($R^2 = 0.14$; Fig. 5).

Pigs Retrospectively Classified as SUS had Improved Production Characteristics During TN Conditions Yet Impaired Thermoregulatory Ability During HS Compared to TOL Pigs

Based on our retrospective classification of TOL and SUS pigs, SUS pigs had increased ADG (1.13 vs. 0.89 kg/d; $P = 0.01$; Table 2) and numerically, but not significantly, increased FI (2.53 vs. 2.42 kg; $P = 0.30$; Table 2) and G:F (0.47 vs. 0.42; $P = 0.21$; Table 2) compared to TOL pigs during P0 and P1. Interestingly, T_R was increased in SUS pigs compared to TOL pigs during both P1 (39.19 vs. 38.87°C; $P < 0.01$; Table 2; Fig. 6A) and also in P2 (40.24 vs. 39.38°C; $P < 0.01$; Table 2; Fig. 6A), and was also accompanied by increased $\Delta BW\%$ (−1.60 vs. −0.77%; $P < 0.01$; Table 2; Fig. 6B) and numerically increased $\Delta FI\%$ (−30 vs. −22%; $P = 0.12$; data not shown). Additionally, SUS pigs had an increased rate of change in T_R compared to TOL pigs (0.12 vs. 0.07 °C/h; $P < 0.01$; data not shown) during P2 (1 to 14 h), indicating SUS pigs not only exhibited a higher maximum T_R during HS, but achieved it at a faster rate than did the TOL pigs.

Figure 3. Correlations between average rectal temperature (T_R) and skin temperature (T_S) of pigs during period (P) 2 (heat stress [HS] conditions; A) and of T_R with respiration rate (RR; B) during P2. Just as with T_R , all T_S and RR data collected 4 h after HS initiation in P2 were condensed into single averages for each experimental unit.

DISCUSSION

Heat stress is an enormous economic burden to the pork industry and animal agriculture as a whole (St-Pierre et al., 2003; Pollmann, 2010). Despite employing HS abatement strategies, HS continues to be a seasonal challenge to animal production efficiency and prevents livestock from expressing their full genetic potential. Notably,

the negative effects of HS on animal agriculture could become increasingly severe (Hoffmann, 2010). Thus, incorporating a HS marker(s) into the genetic selection program may facilitate improved productivity during the warm summer months.

In this study, all pigs had markedly increased body temperature indices, indicating an activated thermoregulatory response to the acute heat load. The magnitude of the thermoregulatory response to HS has potential to be predicated based on intrinsic thermoregulatory set points, as $TN T_R$ positively correlated with $HS T_R$, a phenotype reproducible later in life (Graves et al., 2018). Surprisingly, the T_R response was highly variable among pigs during HS and variation was notably larger in HS than in TN conditions with some animals demonstrating minimal to no T_R increase during HS compared to TN conditions. This high degree of variation within individuals suggests the T_R response is a complex phenotype regulated in part by multiple independent or interdependent factors influenced by environment.

Altering FI is a major mechanism for thermoregulation in pigs as a physiological strategy to reduce metabolic heat production (Bianca, 1976; Blaxter, 1989; Collin et al., 2001; Baumgard and Rhoads, 2013). Feed intake and the associated thermic effect of feeding's contribution to whole body thermal energy has been demonstrated using TN pair-fed models, in which pigs pair-fed to HS counterparts have decreased T_R ($\sim 0.5^\circ\text{C}$) relative to pigs fed ad libitum in the same TN conditions (Pearce et al., 2013). In this study, as expected, FI was reduced during HS, although the relationship between T_R with decreased FI was also highly variable between individuals, suggesting that FI and T_R (while related) are governed by partially independent mechanisms during HS. While not specifically

Table 2. Effects of retrospective classification and environment on thermoregulatory indices and production variables for growing pigs during the study

Parameter	TOL ¹		SUS ²		SEM	P		
	Period 1 ³	Period 2 ⁴	Period 1	Period 2		Class ⁵	Period	Class*Period ⁶
T_R ⁷ , °C	38.87 ^a	39.38 ^c	39.19 ^b	40.24 ^d	0.04	<0.01	<0.01	<0.01
$HS T_R$ slope ⁸	-	0.07	-	0.12	0.01	<0.01	-	-
T_S ⁹ , °C	36.31	41.98	36.98	42.58	0.18	<0.01	<0.01	0.80
RR ¹⁰ , bpm	37.7 ^a	93.3 ^b	40.9 ^a	108.7 ^c	2.3	<0.01	<0.01	<0.01
FI ¹¹ , kg	2.42	1.85	2.53	1.74	0.09	0.43	<0.01	0.18
BW	83.7	83.1	84.7	83.2	0.6	0.03	0.41	0.51

¹Tolerant ($n = 50$) ²Susceptible ($n = 50$) ³Thermoneutral (TN) conditions ⁴Heat stress (HS) conditions ⁵Classification of TOL or SUS; based on HS rectal temperature (T_R ; i.e., higher and lower $HS T_R$ were considered reflective of HS susceptibility or tolerance, respectively) ⁶Classification by period interaction ⁷Rectal temperature ⁸ $HS T_R$ slope ($^\circ\text{C}/\text{h}$) ⁹Skin temperature ¹⁰Respiration rate, breaths per minute ¹¹Feed intake ^{a-d}Means with different letters differ ($P \leq 0.05$)

Figure 4. Correlations between average rectal temperature (T_R) of pigs during period (P) 1 (thermoneutral [TN] conditions) and P2 (heat stress [HS] conditions); A) and of TN T_R with change (Δ) in T_R (B). All TN T_R 's recorded during P1 were condensed into a single average to represent each individual pig's basal core temperature. Rectal temperatures recorded 4 h after HS initiation were condensed into an average to represent core body temperature during P2. The difference in core body temperature (ΔT_R) was calculated by subtracting TN T_R from the HS T_R .

Figure 5. Correlations between the percent change (Δ) in feed intake (FI) and the Δ BW.

addressed in this study, perhaps this variability could be attributed in part to mitochondrial function (Brand, 2005) or mechanisms regulating appetite control (Wynne et al., 2005), but future studies are needed to fully elucidate their involvement during HS.

Figure 6. Thermoregulatory ability of pigs retrospectively classified as tolerant (TOL) and susceptible (SUS) to HS during period (P) 1 (thermoneutral [TN] conditions) and P2 (heat stress [HS] conditions). Each gilt's tolerance to the heat load was classified on the basis of HS rectal temperature (T_R ; i.e., higher and lower HS T_R were considered markers of HS susceptibility or tolerance, respectively). For each of the five replications, the 10 most TOL ($n = 50$) and SUS ($n = 50$) were identified and allocated to their respective retrospective treatments for respective retrospective treatments for T_R (A) and the percent change in BW (Δ BW; B) data analysis. ^{a-d}Values with differing superscripts denote differences ($P \leq 0.05$) between treatments.

Surprisingly, we observed only a marginal association between Δ FI% and Δ BW% from P1 to P2. Some pigs even gained weight while others lost weight despite similar FI during the acute heat challenge (Fig. 3), again highlighting the variability in the HS response between individuals. Furthermore, animals representing the extremes with respect to Δ FI% had strikingly similar Δ BW% during P2 (Fig. 3). Reasons for this are unclear, but may pertain to the amount of water consumed during the acute heat challenge. However, we have previously observed similar hematocrits, a crude measure of hydration, between TN and HS pigs (Boddicker et al., 2014; Pearce et al., 2015). Another potential explanation is variation in digesta passage rates during HS. Heat-stressed pigs are thought to have improved digestibility (Collin et al., 2001; Cosgrove et al., 2002), which is attributed to slower solids passage rate (Christopherson and Kennedy, 1983), but whether or not this contributes to the variation in production responses (i.e., Δ BW) during acute HS will require further investigation.

Intriguingly, we observed weak associations between TN production variables and their changes in response to acute HS. For example, TN FI and $\Delta\text{FI}\%$ as well as ADG and $\Delta\text{BW}\%$ were poorly related ($R^2 = 0.12$ and 0.03 , respectively). Thus, traditionally utilized TN production variable measurements (FI and ADG) actually appear to have low predictive value of the magnitude of $\Delta\text{FI}\%$ and $\Delta\text{BW}\%$ during acute HS. However, when comparing the extremes on the basis of thermoregulation, SUS pigs performed better with ADG under TN conditions, but were more sensitive to the acute HS exemplified through the increase loss of BW as compared to TOL pigs (Table 2 and Fig. 6B).

One factor that inherently decreases pig tolerance to HS is the genetic selection emphasis that has been placed on economically important production traits (Nienaber and Hahn, 2007). In particular, improved lean tissue accretion rates are accompanied by increased basal heat production (Brown-Brandl et al., 2004). Our data corroborate previous studies as SUS pigs (those having higher T_R during HS) had better ADG and numerically increased G:F compared to TOL during TN conditions. Despite an inadvertent reduction in thermotolerance in current high producing commercial lines, it does appear that genetic control over specific phenotypes are seasonally or environmentally influenced (Zumbach et al., 2008). Furthermore, selection for improved growth has deleterious consequences on productivity in specific environmental conditions, as evidenced by a negative genetic correlation of growth or farrowing rate with heat tolerance (Zumbach et al., 2008; Bloemhof et al., 2012). This agrees with ruminant reports as dairy cows and sheep selected for improved milk production are more sensitive to increases in temperature-humidity indices (Ravagnolo and Misztal, 2000; Bohmanova et al., 2005; Finocchiaro et al., 2005).

Few previous studies have intensely collected both thermoregulatory indices and production traits simultaneously; thus the relationships between the aforementioned parameters are ill-defined. This study establishes that a pig's thermoregulatory response to HS appears to be partially set prior to experiencing a heat load, evident by the fact that TN T_R is predictive of T_R and ΔT_R during an acute HS challenge. Comparing T_R in pigs retrospectively classified as "tolerant" or "susceptible" based on thermoregulatory parameters under acute HS indicates the potential predictability of the HS response, in terms of thermoregulation, as ΔT_R and the T_R rate of change were exacerbated to a greater degree in SUS than TOL classified pigs.

Based on the above observations, animals having a low core temperature during TN conditions could be presumed to be most tolerant to HS. While true with regard to the thermoregulatory response, from a production perspective, classification of TOL or SUS to HS should not be determined based solely on thermoregulatory indices (e.g. T_R and RR). For example, critical production efficiency parameters (FI and BW), while severely vulnerable to HS, are not necessarily related to the thermoregulatory response during HS. In other words, thermoregulatory indices are not accurate predictors of production responses during acute HS.

If current genetic selection methods for economically important production traits continue, sensitivity to HS will ostensibly intensify. In dairy cows, genome-wide association studies have discovered single nucleotide polymorphisms (SNP) associated with T_R , but, more importantly, none of the identified SNP were linked with valued production traits (Dikmen et al., 2013). Specific SNP in the HSP70A1A (heat shock 70 kDa protein 1A) gene have even been shown to alter thermoregulatory indices (T_R and RR) without compromising milk yield (Xiong et al., 2013). Furthermore, dairy cows genomically predicted to be heat tolerant have improved productivity and T_R in response to HS compared to those deemed susceptible (Garner et al., 2016). Thus, improved thermotolerance does not necessarily need to be accompanied by blunted production.

In pigs, thermoregulatory and production efficiency responses to HS also appear to be controlled by different genomic regions, suggesting that maintenance of production efficiency during HS is a complex, multifactorial trait (Kim et al., 2018). Indeed, selecting animals with a "tolerant" phenotype based separately on thermoregulatory capacity or production efficiency may not ultimately increase the swine industry's resilience to HS. This is especially true for single, economically important variables, such as feed efficiency, because the single trait only represents one component of an organism, which could potentially undermine other variables or "robustness" in response to environmental insults (Friggens et al., 2017).

Importantly, results from this study encompass responses only to acute HS and may differ between pre- and postpubertal pigs. The types of HS that plague production agriculture are typically more chronic and episodic throughout the summer. Thus, future studies are needed to evaluate phenotypic responses to chronic and repeated HS, and also to consider periods of recovery following HS,

in order to fully understand the complexity of the HS response.

CONCLUSION

In the current study, we explicated that thermoregulatory ability does not predict productivity during acute HS in pigs. Interestingly, however, individual capacity to thermoregulate during HS can be predicted based on TN thermoregulatory parameters (e.g., TN T_R). In addition, $\Delta FI\%$ did not confer a proportional relationship to $\Delta BW\%$ during an acute heat challenge. Importantly, the variation of multiple biological factors, phenotypic and genotypic, need to be taken into account to address the complex multifactorial nature of HS tolerance and to ultimately bolster the pork industry's resilience to HS.

Conflict of interest statement. This project was supported by the National Pork Board. Any opinion, findings, conclusions or recommendations expressed in this publication are those of the authors and do not necessarily reflect the view of the National Pork Board. No conflicts of interest, financial or otherwise are declared by the author (s).

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Animal Science* online.

ACKNOWLEDGMENTS

We would like to acknowledge the assistance of Theresa Johnson, Candice Hager, Matt Garrick, Sarah Edwards, Christy Calderwood, Kelsi Young, Kenton Doty, Brittney Yehling, Marley Dobyns, Sterling Schnepf, Erin Nolan, Alexis Patinos, Briar Tenold, Morgan Vanderlind, and Chris Almond for assistance in collecting temperature and production data.

LITERATURE CITED

- Baumgard, L. H., and R. P. Rhoads. 2013. Effects of heat stress on postabsorptive metabolism and energetics. *Annu. Rev. Anim. Biosci.* 1:311–337. doi:10.1146/annurev-animal-031412-103644
- Bianca, W. 1976. The significance of meteorology in animal production. *Int. J. Biometeorol.* 20:139–156. doi:10.1007/BF01553047
- Blaxter, K. L. 1989. *Energy metabolism in animals and man*. New York: Cambridge University Press, Cambridge England.
- Bloemhof, S., E. H. van der Waaij, J. W. Merks, and E. F. Knol. 2008. Sow line differences in heat stress tolerance expressed in reproductive performance traits. *J. Anim. Sci.* 86:3330–3337. doi:10.2527/jas.2008-0862
- Bloemhof, S., A. Kause, E. F. Knol, J. A. M. Van Arendonk, and I. Misztal. 2012. Heat stress effects on farrowing rate in sows: genetic parameter estimation using within-line and crossbred models. *J. Anim. Sci.* 90:2109–2119. doi:10.2527/jas.2011-4650
- Boddicker, R. L., J. T. Seibert, J. S. Johnson, S. C. Pearce, J. T. Selsby, N. K. Gabler, M. C. Lucy, T. J. Safranski, R. P. Rhoads, L. H. Baumgard, et al. 2014. Gestational heat stress alters postnatal offspring body composition indices and metabolic parameters in pigs. *PLoS ONE* 9:e110859. doi:10.1371/journal.pone.0110859
- Bohmanova, J., I. Misztal, S. Tsuruta, H. D. Norman, and T. J. Lawlor. 2005. National genetic evaluation of milk yield for heat tolerance of united state holsteins. *Interbull Bulletin* 33:160–162.
- Brand, M. D. 2005. The efficiency and plasticity of mitochondrial energy transduction. *Biochem. Soc. Trans.* 33:897–904. doi:10.1042/BST20050897
- Brown-Brandl, T. M., J. A. Nienaber, H. Xin, R. S. Gates. 2004. A literature review of swine heat production. *Trans. ASAE* 47:259–270.
- Christopherson, R. J. and P. M. Kennedy. 1983. Effect of the thermal environment on digestion in ruminants. *Can. J. Anim. Sci.* 63:477–496. doi:10.4141/cjas83-058
- Collin, A., J. van Milgen, S. Dubois, and J. Noblet. 2001. Effect of high temperature and feeding level on energy utilization in piglets. *J. Anim. Sci.* 79:1849–1857. doi:10.2527/2001.7971849x
- Cosgrove, S. J., R. Mosenthin, R. J. Christopherson, B. T. Li, and W. C. Sauer. 2002. Thermogenic and digestive responses of ad libitum fed pigs to $\alpha 2$ -adrenergic stimulation with guanfacin in different thermal environments. *Can. J. Anim. Sci.* 82:79–86. doi:10.4141/A01-026
- D'Allaire, S., R. Drolet, and D. Brodeur. 1996. Sow mortality associated with high ambient temperatures. *Can. Vet. J.* 37:237–239.
- DeShazer, J. A., G. L. Hahn, and H. Xin 2009. Chapter 1: basic principles of the thermal environment and livestock energetics. In: Deshazer, J. A., editor, *Livestock energetics and thermal environment management*. St. Joseph (MI): Am. Soc. Agric. Biol. Eng. p. 181–209.
- Dikmen, S., J. B. Cole, D. J. Null, and P. J. Hansen. 2013. Genome-wide association mapping for identification of quantitative trait loci for rectal temperature during heat stress in holstein cattle. *PLoS ONE* 8:e69202. doi:10.1371/journal.pone.0069202
- Finocchiaro, R., J. B. C. H. M. van Kaam, M. T. Sardina, and I. Misztal. 2005. Effect of heat stress on production in Mediterranean dairy sheep. *Ital. J. Anim. Sci.* 4(Suppl. 2):70–72. doi:10.3168/jds.S0022-0302(05)72860-5
- Friggins, N. C., F. Blanc, D. P. Berry, L. Puillet. 2017. Review: deciphering animal robustness. a synthesis to facilitate its use in livestock breeding and management. *Animal*. 11:1–15. doi:10.1017/S175173111700088X
- Garner, J. B., M. L. Douglas, S. R. Williams, W. J. Wales, L. C. Marett, T. T. Nguyen, C. M. Reich, B. J. Hayes. 2016. Genomic selection improves heat tolerance in dairy cattle. *Sci. Rep.* 6:34114. doi:10.1038/srep34114
- Graves, K. L., J. T. Seibert, A. F. Keating, L. H. Baumgard, and J. W. Ross. 2018. Characterization of the heat stress response in gilts: II. assessing repeatability and association with fertility. *J. Anim. Sci.* In Review.

- Hoffmann, I. 2010. Climate change and the characterization, breeding and conservation of animal genetic resources. *Anim. Genet.* 41 (Suppl 1):32–46. doi:10.1111/j.1365-2052.2010.02043.x
- Intergovernmental Panel on Climate Change (IPCC). 2007. Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge (NY): Cambridge University Press.
- Kim, K. -S., J. T. Seibert, Z. Edea, K. L. Graves, E. -S. Kim, A. F. Keating, L. H. Baumgard, J. W. Ross, and M. F. Rothschild. 2018. Characterization of the heat stress response in gilts: III. Identification of underlying genomic control. *J. Anim. Sci.* In Review.
- Nienaber, J. A., and G. L. Hahn. 2007. Livestock production system management responses to thermal challenges. *Int. J. Biometeorol.* 52:149–157. doi:10.1007/s00484-007-0103-x
- NRC. 2012. Nutrient requirements of swine. 11th rev. ed. Washington (DC): Natl. Acad. Press. doi:10.17226/13298
- Pearce, S. C., N. K. Gabler, J. W. Ross, J. Escobar, J. F. Patience, R. P. Rhoads, and L. H. Baumgard. 2013. The effects of heat stress and plane of nutrition on metabolism in growing pigs. *J. Anim. Sci.* 91:2108–2118. doi:10.2527/jas.2012-5738
- Pearce, S. C., M. V. Sanz Fernandez, J. Torrison, M. E. Wilson, L. H. Baumgard, and N. K. Gabler. 2015. Dietary organic zinc attenuates heat stress-induced changes in pig intestinal integrity and metabolism. *J. Anim. Sci.* 93:4702–4713. doi:10.2527/jas.2015-9018
- Pollmann, D. S. 2010. Seasonal effects on sow herds: industry experience and management strategies. *J. Anim. Sci.* 88(Suppl. 3):9. (Abstr).
- Prunier, A., M. Messias de Braganca, and J. Le Dividich. 1997. Influence of high ambient temperature on performance of reproductive sows. *Livest. Prod. Sci.* 52:123–133. doi:10.1016/S0301-6226(97)00137-1
- Ravagnolo, O., and I. Misztal. 2000. Genetic component of heat stress in dairy cattle, parameter estimation. *J. Dairy Sci.* 83:2126–2130. doi:10.3168/jds.S0022-0302(00)75095-8
- Renaudeau, D., J. L. Gourdiere, and N. R. St-Pierre. 2011. A meta-analysis of the effects of high ambient temperature on growth performance of growing-finishing pigs. *J. Anim. Sci.* 89:2220–2230. doi:10.2527/jas.2010-3329
- Sanz Fernandez, M. V., J. S. Johnson, M. Abuajamieh, S. K. Stoakes, J. T. Seibert, L. Cox, S. Kahl, T. H. Elsasser, J. W. Ross, S. C. Isom, R. P. Rhoads, and L. H. Baumgard. 2015. Effects of heat stress on carbohydrate and lipid metabolism in growing pigs. *Physiol. Rep.* 3:e12315. doi:10.14814/phy2.12315
- St-Pierre, N. R., B. Cobanov, and G. Schnitkey. 2003. Economic losses from heat stress by US livestock industries. *J. Dairy Sci.* 86:E52–E77. doi:10.3168/jds.S0022-0302(03)74040-5
- West, J. W. 2003. Effects of heat-stress on production in dairy cattle. *J. Dairy Sci.* 86:2131–2144. doi:10.3168/jds.S0022-0302(03)73803-X
- Wynne, K., S. Stanley, B. McGowan, and S. Bloom. 2005. Appetite control. *J. Endocrinol.* 184:291–318. doi:10.1677/joe.1.05866
- Xiong, Q., J. Chai, H. Xiong, W. Li, T. Huang, Y. Liu, X. Suo, N. Zhang, X. Li, S. Jiang, et al. 2013. Association analysis of HSP70A1A haplotypes with heat tolerance in Chinese Holstein cattle. *Cell Stress Chaperones* 18:711–718. doi:10.1007/s12192-013-0421-3
- Zumbach, B., I. Misztal, S. Tsuruta, J. P. Sanchez, M. Azain, W. Herring, J. Holl, T. Long, and M. Culbertson. 2008. Genetic components of heat stress in finishing pigs: parameter estimation. *J. Anim. Sci.* 86:2076–2081. doi:10.2527/jas.2007-0282