

Title: Impact of in utero heat stress on subsequent lactational performance and performance of offspring -
NPB project #14-133 Revised

Investigator: Michelle L. Rhoads

Institution: Virginia Polytechnic Institute and State University

Date Submitted: 11-19-15

Industry Summary:

This experiment evaluated the effects of heat stress across multiple generations. In a previous experiment, pregnant gilts were housed in either heat stress or thermoneutral (control) conditions for the entirety of gestation. Female offspring from those pregnancies (F1 generation) were retained, grown to breeding age and then inseminated. The data collection phase for the current experiment began at farrowing and specifically included: 1) post-farrowing lactational measurements, and 2) measurements of growth and carcass quality of offspring (F2 generation). The weigh-suckle-weigh method was used to evaluate the milk production of the F1 generation approximately 19 days after their first farrowing. The results of the weigh-suckle-weigh procedure indicated that milk production did not differ between dams based upon exposure to heat stress in utero. Some aspects of the milk nutrient composition were affected by in utero treatment. Protein content tended to be higher in milk from dams that were heat stressed in utero. Conversely, lactose content was lower in milk from dams that were heat stressed in utero. Milk fat, solids non-fat and somatic cell count did not differ based upon in utero treatment. At the time of weaning, a subset of offspring (male and female) from these litters were retained and grown to slaughter weight in mixed pens under identical management and environmental conditions. Thus, these pigs were the offspring of gestationally heat stressed dams (OgHS) or the offspring of gestationally thermoneutral dams (OgTN). The environment which the dams were exposed to while they were developing in utero did not impact growth of their offspring to market weight. Days of age and live weight at the time of slaughter did not differ between treatment groups, indicating that the number of days needed to reach a similar market weight was not affected by treatment. Interestingly, carcass analysis after 24 hrs post-mortem showed that the OgHS tended to have greater backfat and dressing percentage. There were no detectable differences in loin eye area or lean percentage. The tendency for greater adiposity as indicated by increased backfat thickness indicates that transgenerational effects of in utero heat stress may be diluted, but still evident. These findings suggest that the effects of heat stress on production go beyond the immediate impacts that can be easily measured, indicating that the financial losses associated with heat stress are generally underestimated.

These research results were submitted in fulfillment of checkoff-funded research projects. This report is published directly as submitted by the project's principal investigator. This report has not been peer-reviewed.

For more information contact:

National Pork Board • PO Box 9114 • Des Moines, IA 50306 USA • 800-456-7675 • Fax: 515-223-2646 • pork.org

Key Points:

- Exposure of piglets to heat stress while in utero has long-lasting effects. For females, this in utero insult results in altered milk composition after first farrowing.
- Milk production as assessed by weigh-suckle-weigh did not differ between females exposed to heat stress in utero versus those that were not.
- Offspring of dams that were heat stressed in utero tended to have greater backfat and dressing percentage at slaughter. These results are the first to indicate that heat stress experienced during gestation can affect multiple generations of swine (may be direct effect or a consequence of altered milk composition).
- In utero heat stress of dams did not affect market weight, days to market weight, loin eye area or lean percentage of offspring at slaughter.

Contact Information:

Michelle Rhoads, Ph.D.

Department of Animal & Poultry Sciences

Virginia Polytechnic Institute & State University

3450 Litton-Reaves Hall (0306)

Blacksburg, VA 24061

Phone: 540-231-4740

rhoadsm@vt.edu

Keywords: heat stress, gestation, gilt, milk, lactation, growth, carcass

Scientific Abstract:

Previous research in the area of gestational heat stress (gHS) has shown that pigs exposed to gHS retain greater adiposity during adolescence and yield carcasses with greater fat:lean content at slaughter compared to pigs under thermoneutral gestational conditions (gTN). The objective of this study was to determine the effects of gHS on the lactational performance of affected gilts (F1 generation), as well as to determine if the effects of gHS are multi-generational and persist into subsequent generations (F2 generation). In the experiment, twenty-four post-pubertal gilts were bred and housed in thermoneutral or heat stressed conditions for the entirety of gestation at the University of Missouri-Columbia. Female offspring of these litters (F1 generation) were then grown to breeding age and transported to the Virginia Tech Tidewater Agricultural Research and Extension Center, where they were bred to farrow in two replicates. The first group farrowed in the spring (March and April) and the second in the summer (July and August) months (n = 16 gHS/SPR; 18 gHS/SUM; 19 gTN/SPR; 15 gTN/SUM). Colostrum samples were collected 15 hr post-farrowing, and milk samples were collected on d 7, 14, and 21 post-farrowing. All milk samples were analyzed for fat (FAT), protein (PRO), solids-non-fat (SNF), lactose (LAC) and somatic cell content. Milk yield was also determined at peak lactation (day 19 ± 1 of lactation). There was no effect of gestational treatment or season of farrowing, nor their interactions, on milk production. Protein content tended to be higher in milk from dams that were heat stressed in utero (P=0.07). Conversely, lactose content was lower in milk from dams that were heat stressed in utero (P<0.05). Milk fat, solids non-fat and somatic cell count did not differ based upon in utero treatment. At weaning, a subset of equal-gender offspring from these litters were retained and grown to slaughter in mixed pens under identical management conditions. The dam's gestational environment did not impact growth of these pigs to market weight. Days of age and live weight at the time of slaughter did not differ between treatment groups, indicating that the number of days needed to reach a similar market weight was not affected by treatment. Carcass analysis after 24 hrs post-mortem revealed a tendency for greater backfat (P=0.11) and dressing percentage (P=0.14) in the offspring of gestationally heat stressed dams compared to the offspring of gestationally thermoneutral dams. There were no detectable differences in loin eye

area or lean percentage. The tendency for greater adiposity as indicated by the backfat thickness suggests that the effects of in utero heat stress are diluted, but still evident, across multiple generations of offspring.

Introduction:

Pork producers suffer exorbitant economic loss during periods of heat stress. Poor sow performance alone accounts for a \$330 million annual loss to the U.S. swine industry (reviewed in Baumgard et al., 2012). Since pork producers expect to replace approximately half of their sows annually, it is important that they have as much performance predicting data as possible for selection of replacement gilts. Research from our laboratories and from the laboratories of our colleagues have shown that, amongst other differences, pigs that experienced in utero heat stress have altered body composition (Johnson et al., 2015a) and a differential response to thermal stress measured as respiration rate and body temperature (Johnson et al., 2015b). The results of these and other previous experiments clearly show that in utero heat stress affects performance of market hogs through the finishing phase. To date, however, no one has shown how in utero heat stress affects maternal characteristics (especially milk quality/production) of the resulting gilts. These maternal characteristics have profound implications for production efficiency and profitability because they directly affect the growth and vigor of the next generation of piglets.

The ultimate objective of this research was to provide information that will assist producers in making the best possible decisions concerning replacement gilts, thereby improving overall production efficiency of the herd. We endeavored to determine if exposure to in utero heat stress has long-term effects on the performance of gilts and their offspring. We hypothesized that exposure to heat stress in utero has long-term effects on gilt maternal performance (especially characteristics of lactation). This potential reduction in maternal performance ultimately affects whole herd performance via direct influence on piglet growth and vigor.

The economic implications of this research are evident because we are striving to mitigate the financial losses that pork producers experience as a result of heat stress. Trans-generational effects (especially as a result of altered milk yield of the dam that was gestated in heat stress) have been largely overlooked and represent a significant opportunity to improve production efficiency through targeted selection of replacement females. This increase in production efficiency alone will improve the competitive advantage of the U.S. pork industry.

Specifically, our objectives were to:

- 1) determine the quantity and quality of milk produced by gilts that experienced heat stress in utero (compared to gilts gestated in thermoneutral conditions), and
- 2) determine if the known effects of in utero heat stress on piglet growth, performance and carcass quality are inherited by the next generation of piglets (trans-generational).

Materials & Methods:

All experimental and animal husbandry procedures were approved by the Institutional Animal Care and Use Committees at the University of Missouri and Virginia Tech.

Production of F1 Generation

Twenty-four post-pubertal gilts (214 ± 11 d of age; Landrace X Large White; Newsham Choice Genetics, West Des Moines, IA) were transported from the University of Missouri Swine Research Complex to the Brody Environmental Center (Columbia, MO). Upon introduction to the Brody Environmental Center, gilts were equally divided between two chambers (n=12 gilts per chamber) and housed in individual gestation stalls (2.4 x 0.6 m). Daily boar exposure commenced the day following chamber introduction. Gilts were artificially inseminated (Landrace X Large White pooled boar semen; NCG) 4.8 ± 0.9 d after introduction.

Heat treatment commenced in one chamber on d 13 after move-in (8.2 ± 1.0 d after breeding). The second chamber was maintained at thermoneutral conditions. The chambers were programmed with 24-h temperature cycles of 18-20°C for the TN room and 28-32°C for the HS room. Relative humidity was not controlled. Temperature and humidity of both the heated and thermoneutral chambers were recorded every 15 minutes by in-room data loggers. Photoperiod in both chambers was maintained at 15 h light, 9 h dark. Both chambers were ventilated with outside air with a minimum of ten air changes per hour (10-14 air changes per hour range; air was not recycled). Gilts in both treatment groups were offered the same amount of the same diet throughout gestation. The diet was a standard corn/soybean meal mixture with appropriate vitamin and mineral supplements formulated to meet maintenance requirements.

At 107.2 ± 0.9 d of gestation, gilts were moved from the environmental chambers into a single farrowing room maintained at thermoneutral conditions. Gilts farrowed in standard farrowing crates and were provided ad libitum feed access throughout lactation. Piglets were processed on d 2 post-farrowing (processing included ear notching, needle teeth clipping, tail docking, and a 2 mL intramuscular injection of dehydrogenated iron dextran). Piglets were weaned at 23.6 ± 1.2 d of age.

F1 Generation Post-weaning Through Breeding

Female F1 piglets (n=124) were retained at weaning and grown in split treatment pens at the University of Missouri South Farm according to standard farm production practices. Gilts were transported to the Virginia Tech Tidewater Agricultural Research and Extension Center (TAREC) in Suffolk, VA, at 189 d post-weaning. At TAREC, gilts from both treatments were co-mingled in group pens (approximately 30 gilts per pen). Gilts were divided into four batch farrow groups (n = 20-25 gilts per breeding group; equal number of gHS and gTN gilts in each breeding) and, prior to breeding, moved into gestation stalls in fan-ventilated barns with no additional heating or cooling provisions. Gilts were synchronized with a top-dress feeding of an oral Altrenogest (Maratrix, Intervet, Millsboro, DE) for 14 d, heat checked by daily boar exposure, and artificially inseminated to purebred Yorkshire boars (Swine Genetics International, Cambridge, IA). Breeding groups were planned so that pregnancy occurred during the spring or summer months. Two spring-farrowing groups (SPR) were bred in early November and early December and farrowed in late February and early April, respectively. Two summer-farrowing groups (SUM) were bred in late March and May, and farrowed in July and August, respectively. Thus, gilts that had been gTN and gHS were exposed to either TN or HS conditions as consequence of season during late pregnancy and farrowing. High and low ambient temperatures were recorded at the TAREC station daily. At approximately d 110 of gestation, gilts were moved into one large environmentally controlled farrowing room.

F1 Generation at Farrowing

Farrowings were attended and piglet birth weights were recorded before first suckle. The number of stillbirths and mummified fetuses were also recorded and those fetuses were weighed. Piglets were weighed again at processing (procedures similar to those described previously), which occurred approximately 15 hours after farrowing.

Milk Production and Quality

A colostrum sample was obtained approximately 15 hours (d 1) following the initiation of farrowing. Milk samples were taken during the transient (d 7) and mature stages (d 14 and 21). In each case, letdown was induced via a 1 mL intramuscular injection of oxytocin (Vedco Inc., St. Joseph, MO). Gilts were hand-milked into collection cups, with milk from all teats represented in the sample. Approximately 10 mL of milk was collected per gilt per collection, although less colostrum was available for collection compared to mature milk. Milk was thoroughly mixed in the collection cup and transferred into vials with a broad spectrum preservative. Samples were refrigerated as recommended (one wk or less) until infrared spectrophotometry analysis was conducted for percent fat (FAT), protein (PRO), lactose (LAC), and solids-non-fat (SNF). Spectrophotometry analysis was conducted by the United DHIA lab (Radford, VA).

Peak milk production was measured at $d 19 \pm 1.4$ of lactation using the weigh-suckle-weigh method as described by Lewis et al., 1978. Briefly, piglets were separated from their dams and allowed no access to creep feed or water. After

50 min of separation from the dam, piglets were weighed, returned to the gilt, and suckling was observed. After suckling ceased (evident as two or more piglets defecting from the udder, or the dam changing positions to prevent piglets from accessing the udder) the piglets were again collected and weighed. This procedure was repeated consecutively nine times, with the first three replicates used to acclimatize the pigs and dams to the stress of handling. Data from these three initial weighings was not included in the analysis. Weights from the final six replicates were used to calculate total milk production.

Offspring Performance

At weaning, two male and two female offspring from each litter were retained and grown in mixed pens to market weight (n= 8 Male Spring OgHS; 10 Female Spring OgHS; 18 Male Summer OgHS; 17 Female Summer OgHS; 16 Male Spring OgTN; 16 Female Spring OgTN; 17 Male Summer OgTN; 17 Female Summer OgTN). Pigs remained in environmentally controlled nurseries for 4-6 weeks after weaning. Body weights were recorded at 13, 17, 21, 23, and 25 weeks of age. Pigs were marketed to S&J Villari Livestock (Warsaw, NC) at 187.4 ± 4.5 days of age. Hot carcass weight and carcass length were recorded. After 24 h in the cooler, carcasses were separated between the 10th and 11th rib and backfat thickness and loin eye area were recorded.

Statistics

For all analyses, values greater than two standard deviations from the mean were considered outliers and excluded. Milk production data was analyzed using the mixed procedure (PROC MIXED, SAS Institute, Inc., Cary, NC). The model included the main effects of gestational treatment (gHS or gTN) and season (spring or summer) as well as interactions of these effects. Days in milk, litter size, and average daily feed intake during lactation were included as covariates.

Milk nutrient composition was also analyzed using the mixed procedure in SAS. The model included the main effects of gestational treatment, season, and date of observation (d 1, 7, 14, or 21) as well as interactions of these effects. Gilt was included as the random effect.

Post-weaning growth of pigs was evaluated as average daily gain, BW at 113.7 ± 0.4 d of age and adjusted d of age at a common market weight. Pig d of age at a common market weight (113.4 kg) was calculated using National Swine Improvement Federation adjustment calculations (NSIF, 2003):

adjusted days = actual age + [(desired weight – actual weight) * (actual age – a)/actual weight],
where a = 50 for barrows, and 40 for gilts.

Post-weaning growth variables were then analyzed for a main effect of treatment using the mixed procedure (PROC MIXED) of SAS (SAS Institute, Inc., Cary, NC). For analyses of average daily gain and BW, d of age was included in the model as a covariate. Carcass characteristics were analyzed for main effects of treatment, gender and the treatment x gender interaction using the PROC-MIXED procedure of SAS with HCW as a covariate. When significant, replicate farrowing group was also included in the model. For all analyses (growth and carcass characteristics), seven covariance structures were tested and the most appropriate was chosen based upon Akaike's information criterion, Akaike's information criterion with correction, and Bayesian information criterion values. Pig nested within litter was used as a random effect. Separation of means was conducted using the Tukey-Kramer with adjustments procedure of SAS. Results are reported as least squares means \pm SEM. Statistical significance was set at $P \leq 0.05$.

Results by Objective:

Objective 1) determine the quantity and quality of milk produced by gilts that experienced heat stress in utero (compared to gilts gestated in thermoneutral conditions)

Environmental Data

Average temperature and relative humidity of the heated and thermoneutral chambers was $31.0 \pm 4.0^\circ\text{C}$ and $78.5 \pm 8.6\%$, and $18.1 \pm 2.1^\circ\text{C}$ and $59.7 \pm 5.3\%$, respectively. Average temperature and relative humidity of the farrowing room was similar to the temperature and humidity of the thermoneutral chambers. Average 24 hour temperature for both treatments is presented in Figure 1. Daily high and low temperature for SPR and SUM are presented in Figure 2. Average high and low temperature for spring farrowings was $12.8 \pm 7.2^\circ\text{C}$ and $-1.6 \pm 5.9^\circ\text{C}$, respectively. Average high and low temperature for summer farrowings was $28.0 \pm 5.1^\circ\text{C}$ and $14.0 \pm 5.4^\circ\text{C}$, respectively. Relative humidity was not recorded.

Milk Production

There was no main effect or interaction of pre-natal or post-natal environment on milk production observed using the weigh-suckle-weigh technique at peak lactation ($P > 0.15$; Figure 3).

Colostrum and Milk Nutrient Composition

In all gilts, percent FAT was lowest at d 21 compared to other observations ($P < 0.01$). Additionally, FAT was higher in gilts that farrowed in SUM compared to SPR ($P < 0.05$; Table 1). There was no main effect of gestational environment ($P = 0.33$), nor was there an interaction between gestational treatment and season of farrowing.

There was an effect of gestational treatment on milk LAC, wherein gHS gilts produced less LAC than gTN gilts ($P < 0.05$). Additionally, SUM gilts produced less LAC than did SPR gilts ($P < 0.01$). All gilts produced lower LAC in colostrum (d 1) than at any other point in lactation ($P < 0.01$). The interactions between gestational environment, season of farrowing, and day of milk collection are presented in Table 2. Throughout lactation, LAC was lower in gHS/SUM compared to gHS/SPR ($P < 0.01$) and gTN/SPR ($P < 0.01$). Percent LAC tended to be lower in milk from gHS/SUM gilts than gTN/SUM gilts ($P = 0.11$).

Milk SNF was greater in SUM than in SPR ($P < 0.01$), as well as in the colostrum of gHS/SUM and gTN/SUM gilts compared transient (d 7) and mature milk (d 14 and 21; $P < 0.01$). Treatment interactions for SNF are presented in Table 3.

There was no effect of season on colostrum and milk PRO content ($P > 0.1$). There was a tendency for gHS gilts to produce greater PRO than gTN gilts ($P = 0.07$; Figure 4). Expectedly, PRO was highest in colostrum in both treatments ($P < 0.01$).

Figure 1. Average 24 hr temperature in MU Brody Environmental Chambers

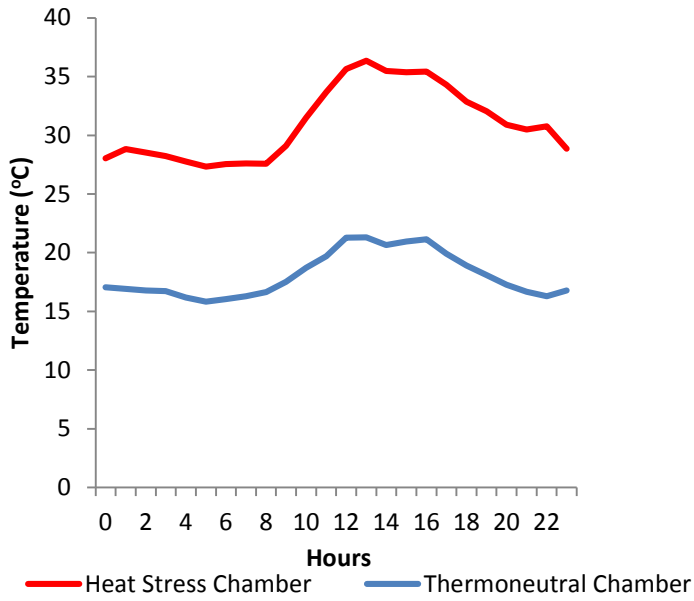


Figure 2. Daily high and low temperatures from breeding through weaning recorded at TAREC for the spring and summer farrowings.

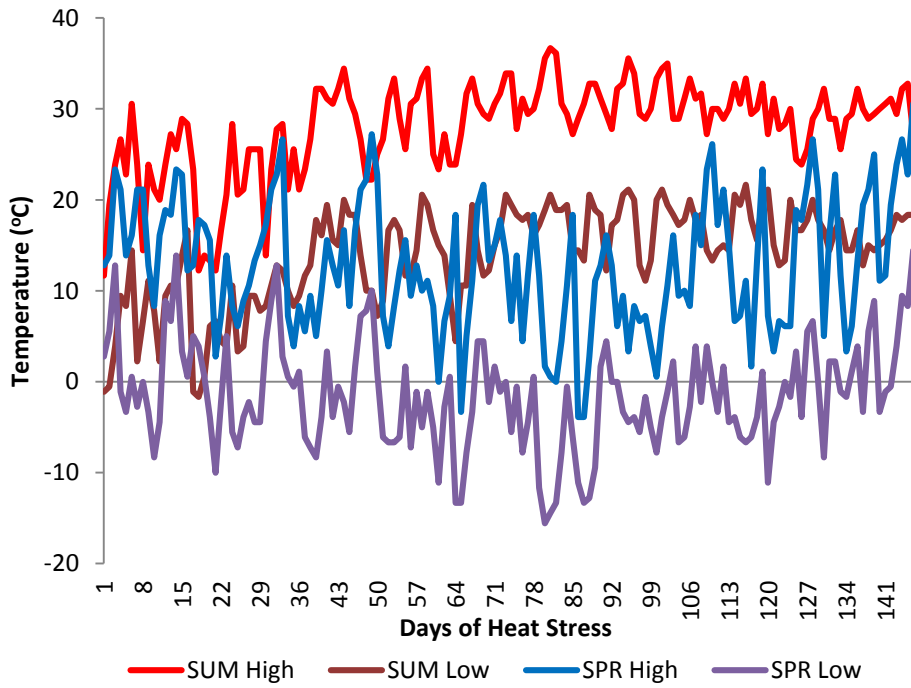


Table 1: Milk Fat Percentage

		d 1	d 7	d 14	d 21	Mean Fat
gHS	SUM	9.09 ± 0.44	9.36 ± 0.26	9.76 ± 0.45	8.18 ± 0.42	9.10 ± 0.26 ^{a, r}
	SPR	8.70 ± 0.49	8.12 ± 0.45	8.48 ± 0.56	6.90 ± 0.44	8.04 ± 0.30 ^b
gTN	SUM	8.77 ± 0.49	9.32 ± 0.29	8.49 ± 0.47	7.42 ± 0.47	8.50 ± 0.28
	SPR	9.09 ± 0.49 ^x	7.91 ± 0.38	8.72 ± 0.60 ^x	6.61 ± 0.40 ^y	8.08 ± 0.30 ^s
Mean Obs.		8.90 ± 0.24 ^x	8.68 ± 0.18 ^x	8.86 ± 0.26 ^x	7.28 ± 0.22 ^y	

* *a, b*: different superscripts within column are different ($P < 0.05$)

* *r, s*: means with different superscripts within column tend to differ ($P < 0.10$)

* *x, y*: different superscripts within row are different ($P = 0.01$)

Table 2: Milk Lactose Percentage

		d 1	d 7	d 14	d 21	Mean Lactose
gHS	SUM	3.96 ± 0.09 ^{a, x}	5.30 ± 0.06 ^y	5.22 ± 0.09 ^{r, y}	5.33 ± 0.10 ^y	4.95 ± 0.05 ^a
	SPR	4.37 ± 0.09 ^x	5.55 ± 0.10 ^y	5.58 ± 0.12 ^y	5.46 ± 0.10 ^y	5.24 ± 0.06 ^b
gTN	SUM	4.03 ± 0.10 ^{a, x}	5.45 ± 0.06 ^y	5.45 ± 0.09 ^y	5.55 ± 0.11 ^y	5.12 ± 0.05
	SPR	4.56 ± 0.10 ^{b, x}	5.49 ± 0.08 ^y	5.71 ± 0.11 ^{s, y}	5.43 ± 0.10 ^y	5.29 ± 0.06 ^b
Mean Obs.		4.23 ± 0.05 ^x	5.44 ± 0.04 ^y	5.49 ± 0.05 ^y	5.44 ± 0.05 ^y	

* *a, b*: different superscripts within column are different ($P \leq 0.05$)

* *r, s*: means with different superscripts within column tend to differ ($P \leq 0.1$)

* *x, y*: different superscripts within row are different ($P < 0.01$)

Table 3: Milk Solid-Non-Fat Percentage

		d 1	d 7	d 14	d 21	Mean SNF
gHS	SUM	13.95 ± 0.43 ^{a, r, x}	11.17 ± 0.09 ^y	11.07 ± 0.11 ^y	11.15 ± 0.12 ^y	11.83 ± 0.14 ^a
	SPR	11.63 ± 0.46 ^s	11.09 ± 0.14	10.75 ± 0.18	11.15 ± 0.12	11.16 ± 0.16 ^b
gTN	SUM	13.25 ± 0.47 ^x	10.96 ± 0.09 ^y	10.89 ± 0.12 ^y	10.93 ± 0.13 ^y	11.50 ± 0.15
	SPR	11.32 ± 0.47 ^s	11.04 ± 0.12	10.97 ± 0.16	11.05 ± 0.11	11.10 ± 0.15 ^b
Mean Obs.		12.54 ± 0.23 ^x	11.07 ± 0.06 ^y	10.91 ± 0.07 ^y	11.07 ± 0.06 ^y	

* *a, b*: different superscripts within column are different ($P < 0.01$)

* *r, s*: means with different superscripts within column are different ($P < 0.05$)

* *x, y*: different superscripts within row are different ($P < 0.01$)

Figure 3. Milk production of gilts observed at 19 ± 1.4 days of lactation.

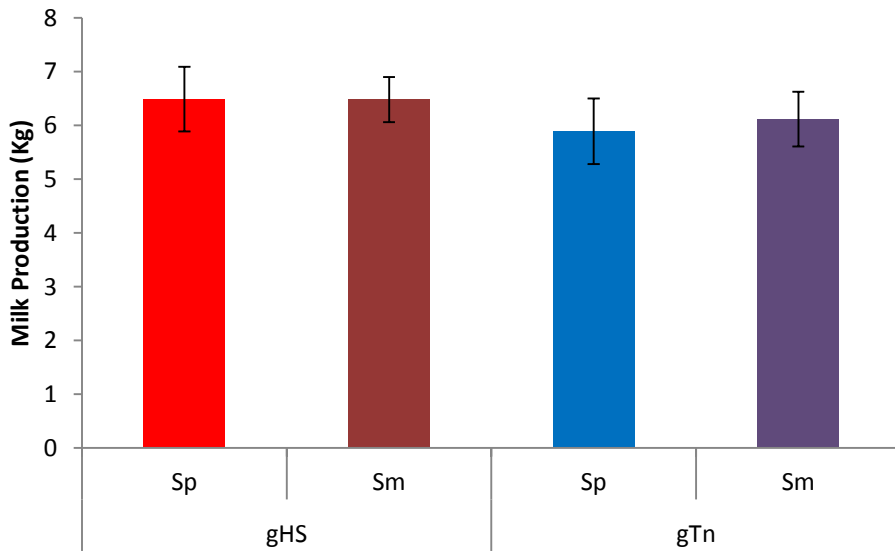
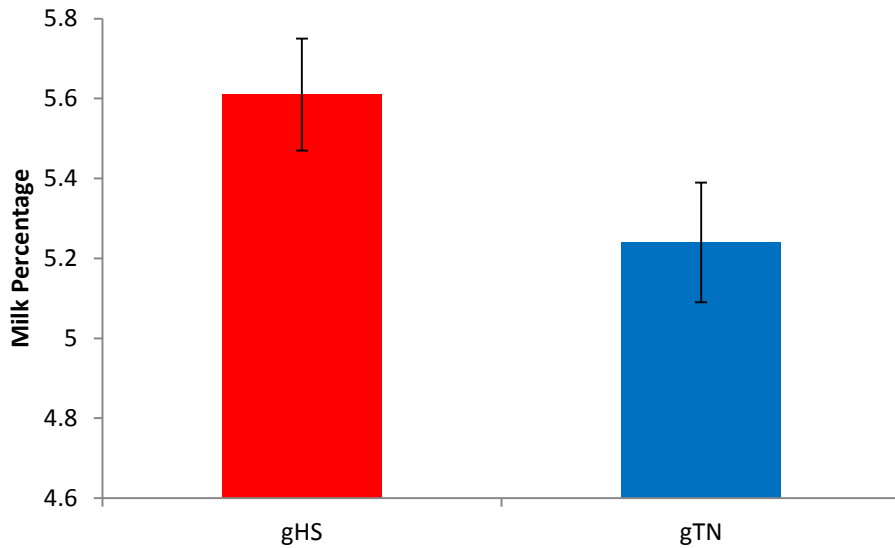


Figure 4. Milk protein percentage in gHS and gTN gilts.



Objective 2) determine if the known effects of in utero heat stress on piglet growth, performance and carcass quality are inherited by the next generation of piglets (trans-generational).

Environment

Environmental conditions imposed during pregnancy to produce the F1 generation are the same as presented for the previous objective. Average high and low temperature for the finishing phase of pigs farrowed in the SPR was $28.5 \pm 3.3^{\circ}\text{C}$ and $15.9 \pm 3.7^{\circ}\text{C}$, respectively. Average high and low temperatures recorded during the finishing phase of pigs farrowed in the SUM was $15.2 \pm 5.1^{\circ}\text{C}$ and $1.9 \pm 5^{\circ}\text{C}$, respectively. Relative humidity was not recorded.

Offspring Growth Performance

Growth of the offspring from gHS and gTN gilts was evaluated from 113.7 ± 0.4 days of age until the day of slaughter. Weight of the pigs did not differ at the beginning (113.7 ± 0.4 days of age) or end (day of slaughter) of the growth analysis period. Likewise, average daily gain during this timespan was not different. Days of age at the time of slaughter also did not differ, indicating that the number of days to market weight was similar for both groups of offspring.

Offspring Carcass Characteristics

Barrows had greater liveweight and hot carcass weight at slaughter compared to gilts ($P < 0.01$). There were no effects of dam gestational environment nor were there interactions with gender for liveweight and hot carcass weight at slaughter ($P > 0.15$).

There were no treatment or gender-related differences in LEA and loin depth ($P = 0.16$). Barrows yielded carcasses with greater BF compared to gilts ($P < 0.01$), and there was a tendency for pigs born to gHS dams to have greater BF than pigs born to gTN dams ($P = 0.11$). There were no gender x treatment interactions for BF thickness ($P > 0.15$). Length of carcasses of pigs born to gHS dams was less than pigs born to gTN dams ($P < 0.01$), and tended to be greater in gilts than in barrows ($P = 0.07$). A gender by treatment interaction for carcass length existed, with barrows

born to gHS dams having the shortest carcass length (82.56 cm) compared to other treatments (84.31 cm F HS, 84.48 cm F TN, and 84.59 cm M TN; $P < 0.05$).

Gilts had greater dressing percentage than did barrows ($P < 0.05$), and there was a tendency for pigs born to gHS dams to have greater dressing percentage than pigs born to gTN dams ($P = 0.14$). Similarly, gilts had a greater LEAN % than did barrows ($P < 0.01$), but there were no differences relating to the dam's gestational environment ($P = 0.21$).

Figure 5: Liveweight at slaughter of gilts and barrows born to either gestationally heat stressed (OgHS) or gestationally thermoneutral (OgTN) dams.

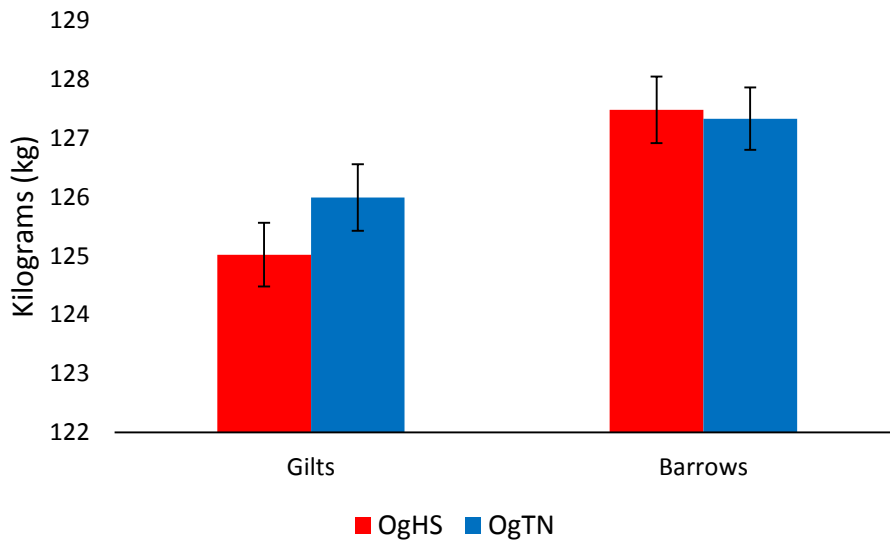


Figure 6: Hot carcass weight of gilts and barrows born to either gestationally heat stressed (OgHS) or gestationally thermoneutral (OgTN) dams.

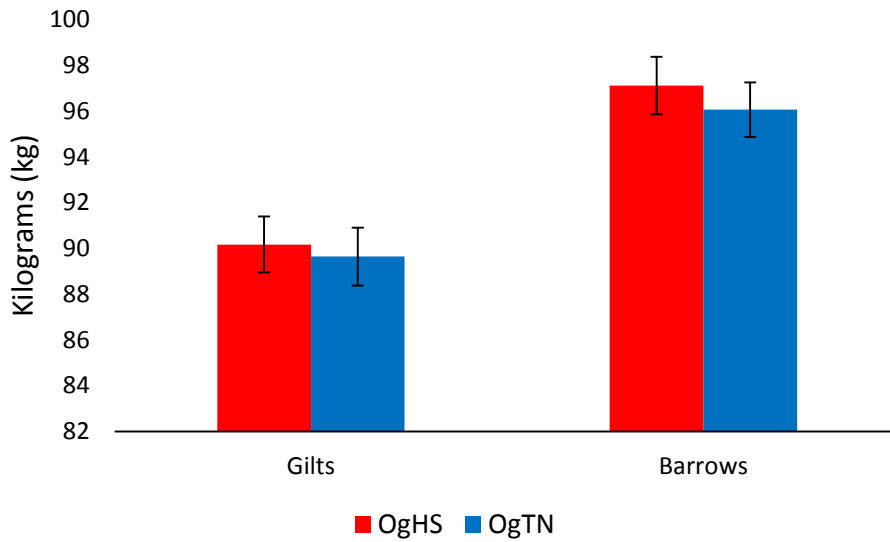


Figure 7: Loin eye area of gilts and barrows born to either gestationally heat stressed (OgHS) or gestationally thermoneutral (OgTN) dams.

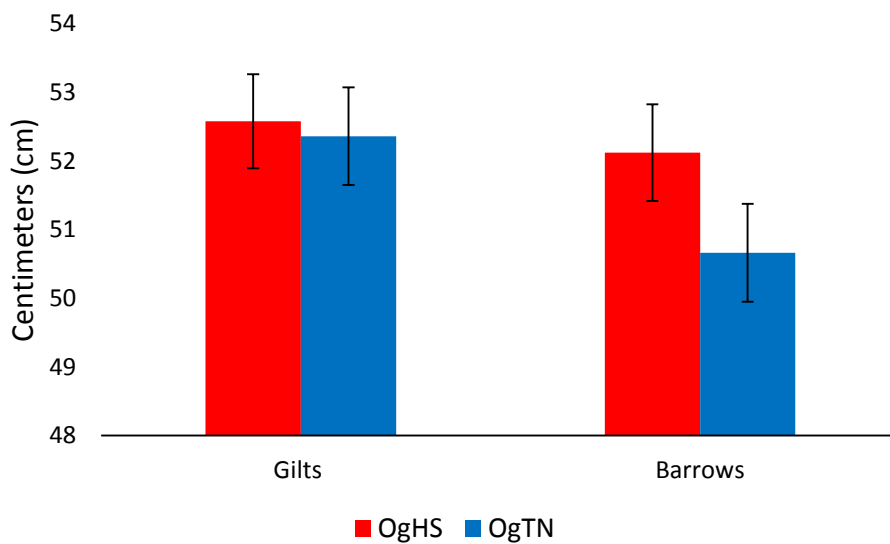


Figure 8: Backfat thickness of gilts and barrows born to either gestationally heat stressed (OgHS) or gestationally thermoneutral (OgTN) dams.

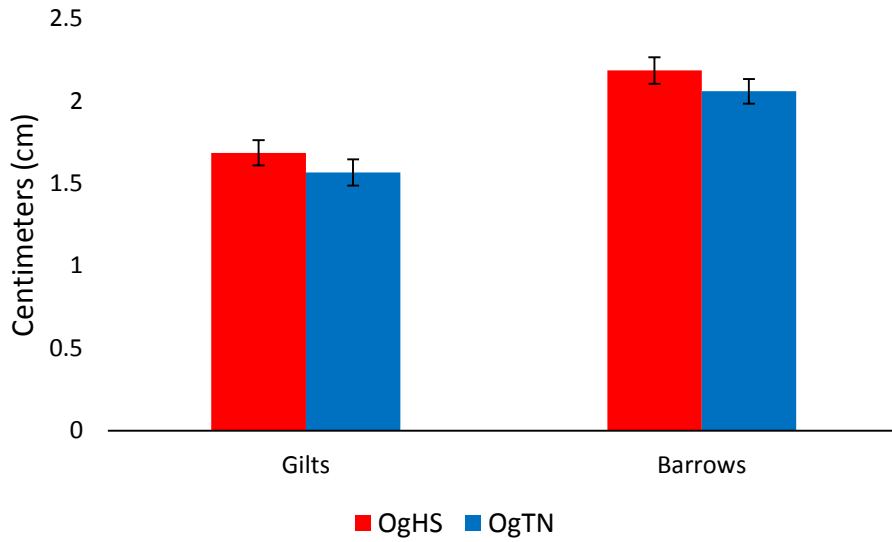


Figure 9: Dressing percentage of gilts and barrows born to either gestationally heat stressed (OgHS) or gestationally thermoneutral (OgTN) dams.

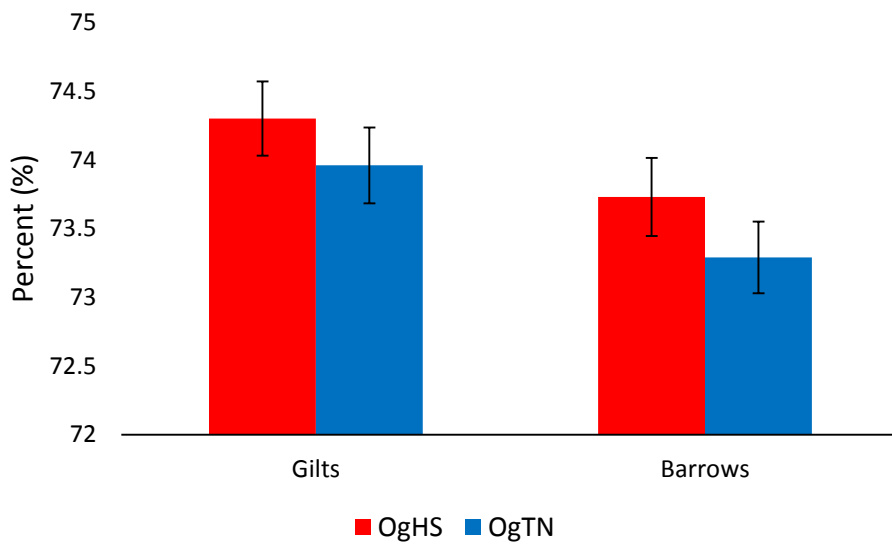


Figure 10: Lean percentage of gilts and barrows born to either gestationally heat stressed (OgHS) or gestationally thermoneutral (OgTN) dams.

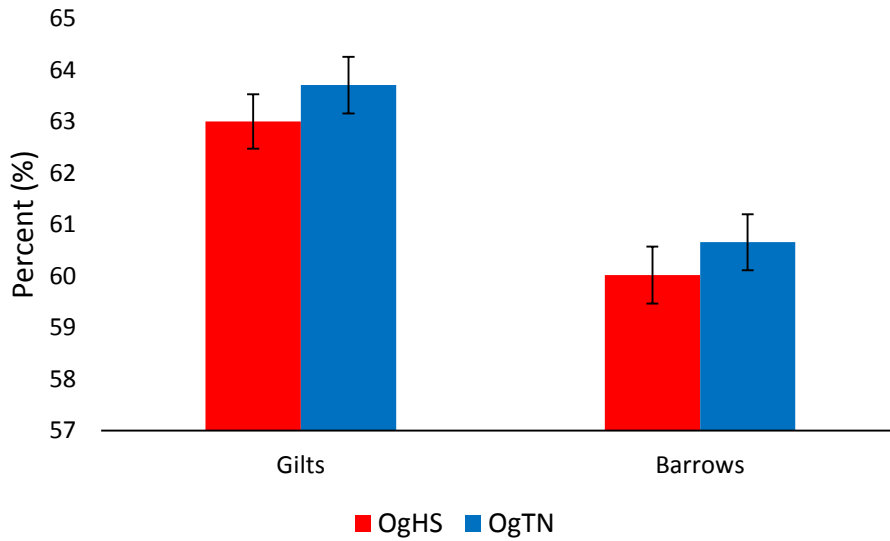
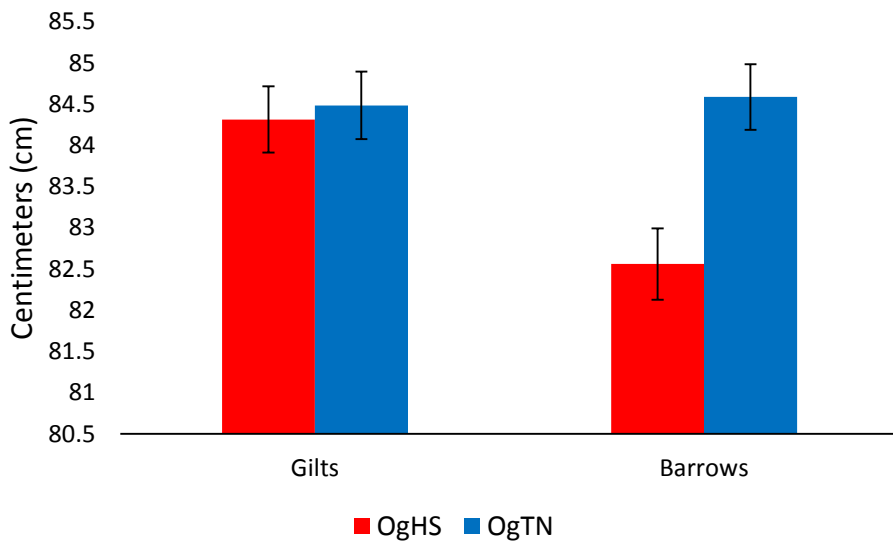


Figure 11: Carcass length of gilts and barrows born to either gestationally heat stressed (OgHS) or gestationally thermoneutral (OgTN) dams.



Discussion by Objective:

Objective 1) determine the quantity and quality of milk produced by gilts that experienced heat stress in utero (compared to gilts gestated in thermoneutral conditions)

This experiment was designed to replicate normal gilt production systems, and as such is highly relevant to breeding swine farms. Gilts are generally expected to farrow their first litter between 10 and 11 mo of age, meaning that female piglets developing in heat stressed dams during the summer months will be exposed to similar conditions during pregnancy when they enter the breeding herd the following year. It would be expected, then, that the differences observed in milk nutrient composition would be representative of on-farm sow production.

In utero environment (heat stress or thermoneutral) did not affect the subsequent milk production of F1 gilt at peak of their first lactation. Previously, heat stress inflicted during late gestation and lactation has been shown to decrease milk production and piglet growth by as much as 35% (Black et al., 1993; Spencer et al., 2003). Although often considered to be a function of reduced feed intake (indirect actions), it is now known that heat stress also reduces milk production through direct actions on the sow's endocrine and mammary systems. For example, heat stress impairs energy reserve mobilization by reducing concentrations of the catabolic cortisol and thyroid hormones (Messias de Braganca et al., 1998). Indeed, daily growth of piglets nursing heat stressed sows is more closely associated with sow weight loss and backfat mobilization than with sow feed intake during lactation (Prunier et al., 1997). Reports in dairy cattle have indicated decreased proliferation and increased apoptosis of mammary epithelial cells under heat stress (Du et al., 2008; Tao et al., 2011). These results have as of yet not been repeated in swine.

Even though gHS did not affect milk production in the present study, Tao and Dahl (2013) cite evidence that that poor adolescent growth coupled with increased pre-pubertal fat accumulation negatively correlates with mammary parenchyma DNA and milk production in dairy heifers, and theorize that gHS may in fact decrease milk production.

Heat stress at the time of farrowing increased milk fat content while decreasing milk lactose. Similar reductions in milk lactose during heat stress have been reported previously in dairy cows (Rhoads et al., 2009; Wheelock et al., 2010), but are also observed during pair-feeding of thermoneutral cattle suggesting that the reduction in milk lactose is likely a result of the reduction in feed intake rather than a direct result of heat stress.

However, the increased FAT percentage observed during summer is at odds with previous studies. The majority of studies indicate either no effect (Prunier et al., 1997; Renaudeau and Noblet, 2001) or a slight decrease in percent milk fat during heat stress (Schoenherr et al., 1989; Renaudeau et al., 2003). However, differences in experiment design make direct comparisons to these studies difficult. Notable differences include use of multiparous sows (Schoenherr et al., 1989; Renaudeau and Noblet, 2001; Renaudeau et al., 2003) and having inflicted heat stress either in late-gestation (Schoenherr et al., 1989), at farrowing (Prunier et al., 1997; Renaudeau and Noblet, 2001) or in mid-lactation (Renaudeau et al., 2003). It is unknown what effect, if any, the duration of heat stress may have on milk fat secretion. More studies will be required to understand the effects of acute vs chronic heat stress on fat content of milk.

There was no effect of season on milk protein content, which is consistent with previous reports (Renaudeau et al., 2003). Indeed, Renaudeau and others (2003) determined that the mammary preferentially selects essential amino acids at the expense of non-essential amino acids (which may be synthesized from essential amino acids) to maintain protein synthesis during heat stress. Amino acids were not measured in the present study.

Objective 2) determine if the known effects of in utero heat stress on piglet growth, performance and carcass quality are inherited by the next generation of piglets (trans-generational).

Carcass analysis of market pigs exposed to gHS has revealed an increase in the rate of lipid accretion (292 g/d vs 220 g/d) and a 95% increase in the ratio of lipid:lean protein accretion (Johnson et al., 2015a). Likely, this increased body adiposity is due to increased circulating insulin concentrations. Pigs exposed to gHS show 33% greater insulin levels compared to pigs gestated under TN conditions (Boddicker et al., 2014). Similar hyperinsulinemia and body adiposity has been found in calves exposed to gHS in late gestation (Tao and Dahl, 2013).

The carcass characteristics of pigs developing in either gHS or gTN of pigs in this study indicate that the effects of gestational hyperthermia are multi-generational. Indeed, pigs born to gHS dams tended to show greater carcass

adiposity, as indicated by greater BF thickness at slaughter. Although not statistically significant ($P = 0.21$), there was also numerically greater carcass LEAN % of pigs born to gTN dams which is consistent with effects previously observed in the F1 generation (Johnson et al., 2015a).

The reduced carcass length of only barrow OgHS pigs is interesting. Stahly and Cromwell (1979) reported a positive linear effect of increasing ambient temperature on carcass length. The greater body length of swine grown under heat stress conditions, as well as the reduced carcass length of swine grown during cold stress, likely exists as a mechanism through which the animal alters their surface area:body mass ratio in an effort to conserve or dissipate heat. It is also known that gHS development can influence body development. Alexander and Williams (1971) showed that developmentally heat stress lambs exhibited comparatively longer bodies with larger skulls, brains, kidneys, and pituitary and adrenal glands, but smaller livers, thyroids, and bicep muscles. A longer carcass length would therefore be anticipated in OgHS pigs. It is unknown why the carcass length of only barrow OgHS were affected, and why their carcass length was reduced, and not increased.

At this time, it is unknown if the multi-generational effects are due to altered maternal physiology or as a function of true epigenetic modifications to the animal's epigenome. For example, studies in ruminants have shown that heat stress during gestation reduces placental size, blood flow, and oxygen and glucose transfer to the fetus (Bell et al., 1987; Thureen et al., 1992). This results in a smaller fetus that is hypoxic and hypoglycemic compared to fetuses developing under TN conditions (Reynolds et al., 1985). These smaller fetuses also show discrepancy in organ development, with the liver being most severely affected by gHS (Reynolds et al., 1985; Dreiling et al., 1991). When adjusted for day of gestational age, Reynolds and others (1985) found that the livers from heat stressed bovine fetuses weight only 61% of livers from thermoneutral fetuses (173 g vs 284 g, respectively). These livers also showed reduced total RNA and protein content, possibly indicating a reduced capacity for protein synthesis throughout life. Liver weight and liver function were not measured in this study, but if affected by gHS could be one means by which metabolism and physiology are altered.

Although yet to be proven, it is assumed that the response of mammals to developmental hyperthermia is at least partially the result of epigenetic modifications. The potential for epigenetic modifications are intriguing because many such alterations can be passed to the next generation. The present experiment was not designed to determine whether the differences in physiology of the F2 generation are due to altered maternal physiology or imprinted epigenetic modifications. Certainly, more research will be required to better define and understand the effects of gHS across generations.

References

- Alexander, G. and D. Williams. 1971. Heat stress and development of the conceptus in domestic sheep. *Journal of Agricultural Science* 76:53-72.
- Baumgard, L. H., R. P. Rhoads, M. L. Rhoads, N. K. Gabler, J. W. Ross, A. F. Keating, R. L. Boddicker, S. Lenka, and V. Sejian. 2012. Impact of Climate Change on Livestock Production. in *Environmental Stress and Amelioration in Livestock Production*. V. Sejian, S. M. K. Naqvi, T. Ezeji, J. Lakritz, and R. Lal, ed. Springer-Verlag, Berlin Heidelberg.
- Bell, A. W., R. B. Wilkening, and G. Meschia. 1987. Some aspects of placental function in chronically heat-stressed ewes. *Journal of developmental physiology* 9(1):17-29.
- Black, J. L., B. P. Mullan, M. L. Lorsch, and L. R. Giles. 1993. Lactation in the sow during heat stress. *Livestock Production Science* 35(1-2):153-170.
- 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, and J. W. Ross. 2014. Gestational heat stress alters postnatal offspring body composition indices and metabolic parameters in pigs. *PloS one* 9(11):e110859.
- Dreiling, C. E., F. S. Carman, 3rd, and D. E. Brown. 1991. Maternal endocrine and fetal metabolic responses to heat stress. *J Dairy Sci* 74(1):312-327.
- Du, J., H.-S. Di, L. Guo, Z.-H. Li, and G.-L. Wang. 2008. Hyperthermia causes bovine mammary epithelial cell death by a mitochondrial-induced pathway. *Journal of Thermal Biology* 33(1):37-47.
- Johnson, J. S., M. V. Sanz Fernandez, J. F. Patience, J. W. Ross, N. K. Gabler, M. C. Lucy, T. J. Safranski, R. P. Rhoads, and L. H. Baumgard. 2015a. Effects of in utero heat stress on postnatal body composition in pigs: II. Finishing phase. *J Anim Sci* 93(1):82-92.
- Johnson, J. S., M. V. Sanz Fernandez, J. T. Seibert, J. W. Ross, M. C. Lucy, T. J. Safranski, T. H. Elsasser, S. Kahl, R. P. Rhoads, and L. H. Baumgard. 2015b. In utero heat stress increases postnatal core body temperature in pigs. *J Anim Sci* 93(9):4312-4322.
- Messias de Braganca, M., A. M. Mounier, and A. Prunier. 1998. Does feed restriction mimic the effects of increased ambient temperature in lactating sows? *J Anim Sci* 76(8):2017-2024.
- NSIF. 2003. Swine Improvement Program Guidelines.
- Prunier, A., M. M. de Bragança, and J. Le Dividich. 1997. Influence of high ambient temperature on performance of reproductive sows. *Livestock Production Science* 52(2):123-133.
- Renaudeau, D. and J. Noblet. 2001. Effects of exposure to high ambient temperature and dietary protein level on sow milk production and performance of piglets. *J Anim Sci* 79(6):1540-1548.
- Renaudeau, D., J. Noblet, and J. Y. Dourmad. 2003. Effect of ambient temperature on mammary gland metabolism in lactating sows. *J Anim Sci* 81(1):217-231.
- Reynolds, L. P., C. L. Ferrell, J. A. Nienaber, and S. P. Ford. 1985. Effects of chronic environmental heat stress on blood flow and nutrient uptake of the gravid bovine uterus and foetus. *Journal of Agricultural Science* 104:289-297.
- Rhoads, M. L., R. P. Rhoads, M. J. VanBaale, R. J. Collier, S. R. Sanders, W. J. Weber, B. A. Crooker, and L. H. Baumgard. 2009. Effects of heat stress and plane of nutrition on lactating Holstein cows: I. Production, metabolism, and aspects of circulating somatotropin. *J Dairy Sci* 92(5):1986-1997.
- Schoenherr, W. D., T. S. Stahly, and G. L. Cromwell. 1989. The effects of dietary fat or fiber addition on yield and composition of milk from sows housed in a warm or hot environment. *J Anim Sci* 67(2):482-495.
- Spencer, J. D., R. D. Boyd, R. Cabrera, and G. L. Allee. 2003. Early weaning to reduce tissue mobilization in lactating sows and milk supplementation to enhance pig weaning weight during extreme heat stress. *J Anim Sci* 81(8):2041-2052.
- Stahly, T. S. and G. L. Cromwell. 1979. Effect of Environmental Temperature and Dietary Fat Supplementation on the Performance and Carcass Characteristics of Growing and Finishing Swine. *Journal of Animal Science* 49(6).
- Tao, S., J. W. Bubolz, B. C. do Amaral, I. M. Thompson, M. J. Hayen, S. E. Johnson, and G. E. Dahl. 2011. Effect of heat stress during the dry period on mammary gland development. *J Dairy Sci* 94(12):5976-5986.
- Tao, S. and G. E. Dahl. 2013. Invited review: heat stress effects during late gestation on dry cows and their calves. *J Dairy Sci* 96(7):4079-4093.
- Thureen, P. J., K. A. Trembler, G. Meschia, E. L. Makowski, and R. B. Wilkening. 1992. Placental glucose transport in heat-induced fetal growth retardation. *Am J Physiol* 263(3 Pt 2):R578-585.

Wheelock, J. B., R. P. Rhoads, M. J. Vanbaale, S. R. Sanders, and L. H. Baumgard. 2010. Effects of heat stress on energetic metabolism in lactating Holstein cows. *J Dairy Sci* 93(2):644-655.