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REVIEW ARTICLE

Heat stress in pregnant sows: Thermal responses and subsequent performance of sows and their offspring

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Seasonal infertility is a significant problem in the swine industry, and may be influenced by photoperiod and heat stress. Heat stress during gestation in particular affects pregnancy, resulting in long-term developmental damage to the offspring. This review summarizes what is known about how heat stress on the pregnant sow affects lactation and her offspring. Sows responded to heat stress during gestation with increased rectal temperature, respiration rate, and skin temperature, and tended to reduce their activity—which may have changed their body composition, increasing the adipose-to-muscle ratio. Heat stress during gestation caused temporary insulin resistance during lactation, but this metabolic state did not seem to affect health, lactation, or rebreeding performance of the sow. Heat-stressed sows also presented with a shorter gestation period and reduced litter birth weight, although weaning weights are not affected when these sows are moved to thermoneutral conditions for lactation. The offspring of gestational heat-stressed sows, however, possessed unique phenotypes, including elevated body temperature, greater fat deposition, and impaired gonad development. Thus, gestational heat stress may significantly impact a herd through its effects on sows and their offspring. Further work is necessary to determine the magnitude of the effects across facilities and breeds.

KEYWORDS
body temperature, pig, pregnancy

> *[The] specific effects of heat stress on the life cycle of the sow have significant implications beyond those most-easily recognized during lactation and rebreeding.*

1 | INTRODUCTION

Both photoperiod and heat stress contribute to seasonal infertility on swine farms (Love, 1978; Love, Evans, & Klupiec, 1993; Sevillano, Mulder, Rashidi, Mathur, & Knol, 2016). Initial studies of heat stress primarily focused on the lactating sow because lactation is a period of high metabolic load that sensitizes individuals to environmental temperature (Williams et al., 2013). Heat-stressed sows normally reduce their feed intake (Prunier, Messias de Braganca, & Le Dividich, 1997; Renaudeau et al., 2012), leading to negative energy balance, loss of body condition, and associated reproductive problems related to inadequate ovarian function—i.e., anestrus, long weaning to estrus intervals, low farrowing rates, depressed litter size (Nardone, Ronchi, Lacetera, & Bernabucci, 2006), and reduced milk production, which can negatively affect piglet growth during lactation and their weaning weight (Black, Mullan, Lorschy, & Giles, 1993; Quiniou & Noblet, 1999). The impact of heat stress is not limited to the postnatal period, as it also affects the sow during gestation. For example, heat stress

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Abbreviations: IGF1, Insulin-like growth factor 1; IUHS, in utero heat stress; IUTN, in utero thermoneutral; NEFA, non-esterified fatty acids.

during early pregnancy increased embryo mortality (Edwards, Omtvedt, Tuesman, Stephens, & Mahoney, 1968; Wildt, Riegle, & Dukelow, 1975), which affects farrowing rate and litter size (Nardone et al., 2006), while heat stress in later pregnancy increased the number of stillborn piglets (Edwards et al., 1968; Omtvedt, Nelson, Edwards, Stephens, & Turman, 1971; Wegner, Lambertz, Das, Reiner, & Gauly, 2016) and reduced newborn piglet weight (Lucy et al., 2012b). When analyzed across the entire production cycle of a sow, which includes animal growth, heat stress had a substantial economic impact on the swine industry worldwide (St. Pierre, Cobanov, & Schnitkey, 2003).

Many of the effects of heat stress are readily apparent on-farm, including anestrus, weak or irregular expression of estrus, delayed puberty, irregular estrous cycles, reduced farrowing rates, increased abortion rates, and depressed litter size (Nardone et al., 2006). The long-term effects of heat stress on the sow may be greater since heat stress during pregnancy can cause developmental damage to offspring that is manifested later in life; this phenomenon is not limited to swine, as similar phenotypes were described for humans, rodents, and cattle (Dreier, Andersen, & Berg-Beckhoff, 2014; Tao & Dahl, 2013). Developmental effects tend to be subtle and less easily detected on-farm, especially if brief gestational windows of sensitivity do not coincide with heat-stress conditions during any given pregnancy. In addition, gestational heat stress may imprint the physiology of the sow and affect her performance during lactation and rebreeding. Therefore, the specific effects of heat stress on the life cycle of the sow have significant implications beyond those most-easily recognized during lactation and rebreeding.

Heat stress can be mitigated on-farm using different approaches. For example, evaporative cooling systems decrease the ambient temperature by 5–7°C inside swine barns, depending on the outside temperature and relative humidity. The choice of which barns to cool (breeding/gestation, farrowing, or both) depends on the economic loss if mitigation strategies are not used, and the economic loss depends on the magnitude of the effect on performance, as assessed through controlled research trials. This review addresses the unique thermoregulatory aspects of sows experiencing heat stress during gestation, as well as the effects on the sow during heat stress and latent effects on the sow and her offspring. This information has value from both applied (when to cool pigs in the production cycle and the value of the cooling) and basic (biological mechanisms controlling thermoregulation) scientific perspectives.

2 | HEAT STRESS DURING GESTATION

Studies of heat stress can be performed either on-farm or under controlled conditions within environmental chambers. We use environmental chambers equipped with gestation stalls for most studies at the University of Missouri; each chamber has a 12-pig capacity. The ambient temperature inside the heat-stress chambers is cycled from approximately 25°C to 35°C, while the relative humidity is cycled from approximately 60–90% (Figure 1). Each cycle is 24 hr in length. A greater heat load (higher temperature-humidity index) for pigs in the heat-stress chambers, which is above minimum thresholds for effects on reproduction, can be achieved by cycling both temperature and humidity (Wegner et al., 2016). Thermoneutral conditions are approximately 15–22°C with 60–70% relative humidity, which all pigs are inseminated under. The heat stress is applied through a step-up procedure during early gestation (Figure 1) so as not to cause abortion

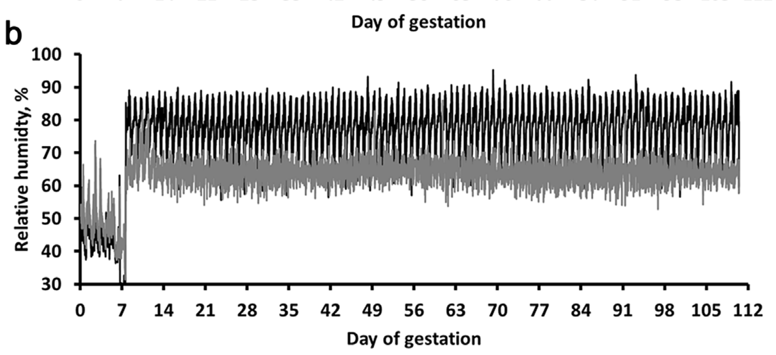

FIGURE 1 Ambient temperature (a) and relative humidity (b) inside heat-stressed (HS) and thermoneutral (TN) Brody Environmental Chambers at the University of Missouri. Temperature and humidity were cycled daily to subject gestating pigs to different environmental conditions

during early pregnancy. Full heat stress is applied after pregnancy diagnosis during the fourth week of pregnancy. We do not apply drippers or fans to sows within the environmental chambers, although the concrete floors afford some opportunity for conductive heat loss. Pigs also manipulate their nipple waters in an attempt to wet their skin and floor, providing another opportunity for evaporative heat loss.

The conditions we apply are the same each day, which is not what sows experience on-farm. Thus, an interesting scientific question that we have not yet explored is if the more erratic climatic conditions that might be experienced on-farm—e.g., a heat wave—create biological responses different from those that we observe under controlled, repetitive conditions.

2.1 | Thermobiology of the gestating sow during controlled heat stress

Pregnant sows under controlled, thermoneutral conditions underwent a progressive decline in body temperature of approximately 0.4°C from the beginning to end of gestation (Figure 2a) (Lucy et al., 2012a). This reduction in body temperature over time is consistent across a number of trials in pigs, but is not typically reported for other animals. When subjected to heat stress, however, this decrease in sow body temperature did not occur to the same magnitude, and a slight increase in body temperature over time was observed after the initial slight decline. By the end of gestation, heat-stressed, and thermoneutral sows differed in body temperature by approximately 0.3°C.

One of the primary mechanisms the pregnant sow used in an attempt to alleviate heat stress was increased respiration rate (Figure 2b). The respiration rate of heat-stressed sows progressively rose with the weeks of gestation, indicating that the metabolic heat production associated with the developing pregnancy was elevated; this pattern was not observed in thermoneutral sows over the same gestation period (Figure 2b). Respiration rate was a more sensitive indicator of heat stress than body temperature, and our work agreed with numerous previous studies that reported greater respiration rate in heat-stressed sows (Liao and Veum, 1994; Spencer, Boyd, Cabrera, & Allee, 2003).

Skin temperature also increased over time in sows that are heat-stressed during gestation as blood was shunted to peripheral circulation (Figure 2c). Based on skin temperature, heat-stressed sows were maximally vasodilated by mid-gestation, so no additional benefits were achieved through shunting to alleviate heat stress after mid-gestation.

Heat-stressed pigs also reduced activity, perhaps as a mechanism to lower heat production associated with movement. When we recorded rooting, sleeping, standing, and sitting behavior during mid-gestation in sows that were either heat-stressed or thermoneutral (Figure 3), we found that heat-stressed sows spent less time rooting (Figure 3a) and more time sleeping (Figure 3b) (Rippe, Lucy, and Safranski, unpublished). They also stood for less time during the day (Figure 3c), and spent more time sitting upright (Figure 3d) compared with thermoneutral sows. When sows were heat stressed during the entire gestation period, we observed greater body weight, greater loin area (by ultrasound exam), and more back fat (by ultrasound exam) at the end of gestation compared to thermoneutral sows (Lucy et al., 2015). Since sows in this study were limit-fed during gestation and had similar intake in both thermal environments, the differences in body weight and composition in heat-stressed sows are instead explained, in part, by their behavioral changes (less standing, more sitting, and more sleeping) that reduced maintenance energy requirements and internal heat production. The behavioral changes could, in theory, also affect the development of musculature associated with movement during pregnancy.

Although heat-stressed sows farrowed approximately 1.5 days earlier than thermoneutral sows (Lucy et al., 2012b), we did not observe any latent effects on farrowing (dystocia, prolonged parturition, or greater need for assistance, for example) in heat-stressed sows that could be explained by reduced activity during gestation. The possibility that reduced activity caused by heat stress during gestation affect farrowing should be investigated further. For example, gestational heat-stressed sows exhibited insulin resistance during lactation (described below), so perhaps insulin resistance was a latent effect of the reduced activity and greater adipose tissue mass during gestation. Specific stages of gestation should also be investigated to determine when the sow is most susceptible to heat stress.

The stall-housed pigs in our trials had limited mobility throughout gestation, so it is possible that they become less active and generated less metabolic heat as their pregnancy progressed. Reduced metabolic heat production associated with reduced activity may explain the

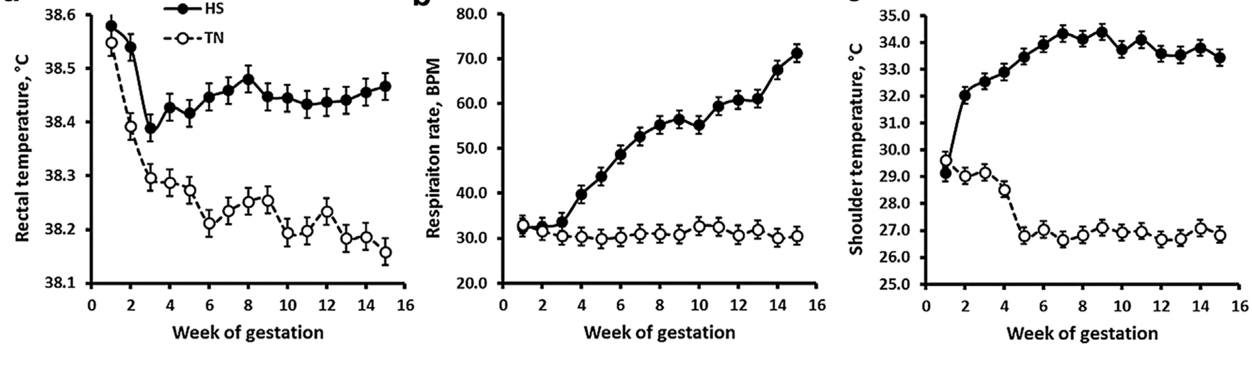

FIGURE 2 Rectal temperature (a), respiration rate (b), and shoulder temperature (c) for sows that were either heat stressed (HS) (27–37°C; 85–55% relative humidity) or thermoneutral (TN) (15–20°C; 60–50% relative humidity) during gestation (Lucy et al., 2012a). BPM, breaths per minute

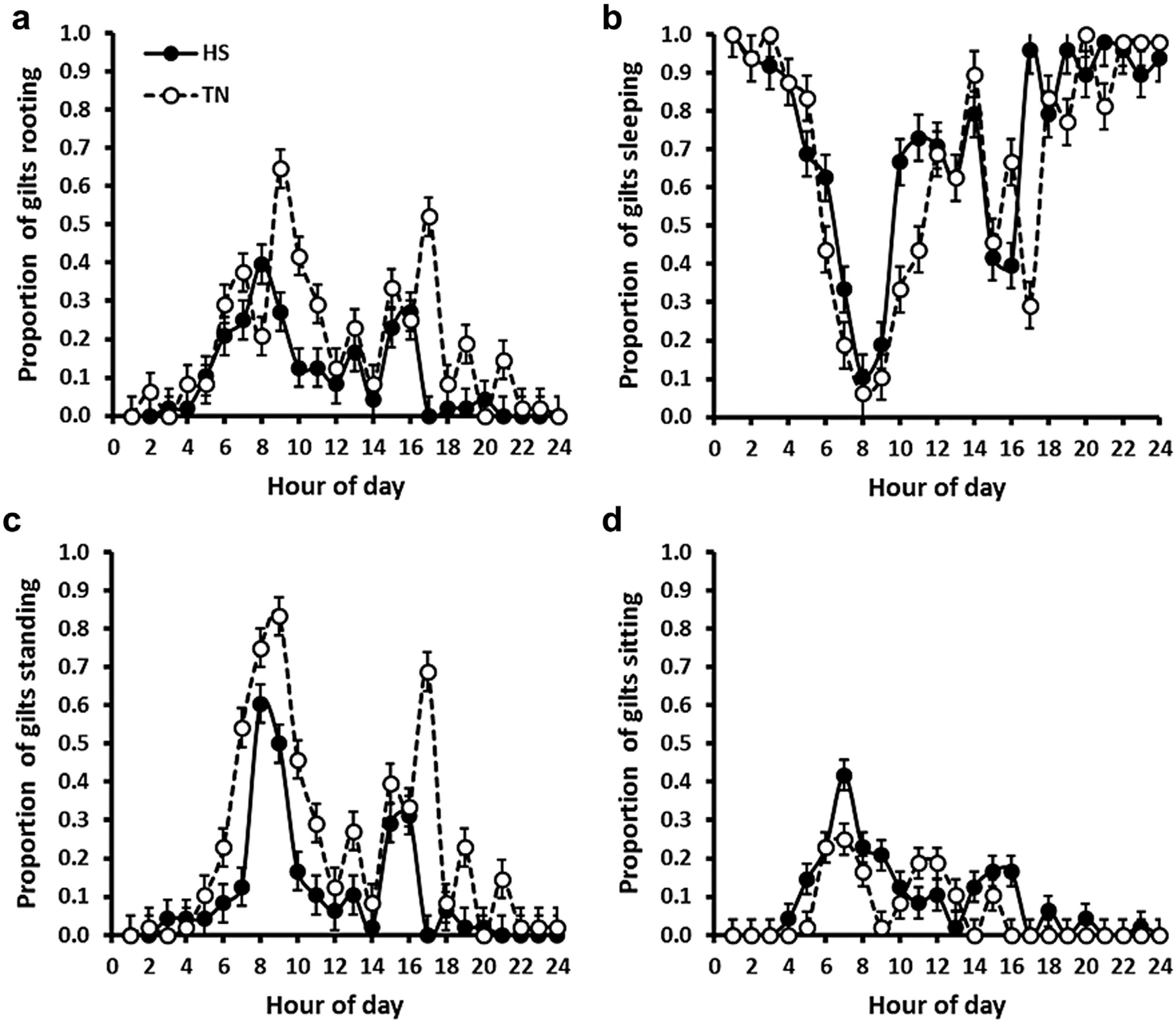

FIGURE 3 Proportion of mid-gestation gilts rooting (a), sleeping (b), standing (c), and sitting (d) during heat stress (HS) (28–34°C, 80–55% relative humidity; *n* = 12) or thermoneutral (TN) (18–22°C, 70–60% relative humidity; *n* = 12) conditions. Greater activity at 08:00 and 16:00 hr were associated with feeding and cleaning of the pens. Heat-stressed gilts spent less time rooting, more time sleeping, less time standing, and more time sitting compared to thermoneutral gilts (Rippe, Lucy, and Safranski, unpublished)

changes we observed. If true, then the differences may be greater in settings where sows are loose-housed throughout gestation. Our data suggest that biological mechanisms can change body temperature set point and reduce body temperature over time. Such changes in body temperature were not associated with appreciable changes in respiration rate, and skin temperatures were reduced, which implied a new temperature set point rather than an artifact of changes in behavior. Perhaps reduced body temperature during gestation is a general adaptation to pregnancy that buffers the fetus from changes in body temperature that could alter developmental patterns.

2.2 | Progesterone in the pregnant sow

Circulating progesterone concentrations were reduced in pregnant gilts subjected to heat stress, particularly during the second half of gestation (Figure 4). Conversely, no consistent effects of heat stress on circulating progesterone were published for cattle, as some studies reported a decrease while others reported no effect or an increase compared to control animals (reviewed by De Rensis & Scaramuzzi, 2003). Thus, the observed effect of heat stress on progesterone production may depend on the nature of the stress (acute or chronic) and whether or not the animal was lactating. Miller and colleagues reported that increasing feed intake increased the metabolic clearance rate of progesterone in gilts (Miller, Foxcroft, Squires, & Aherne, 1999). Sows treated during late gestation, however, did not exhibit a greater metabolic clearance rate of progesterone in response to higher feed intake (Miller, Foxcroft, & Aherne, 2004). Therefore, the differences in progesterone for heat-stressed versus thermoneutral gilts that we observed (Figure 4) may not have been caused by differences in progesterone metabolism. Instead, the decrease in circulating

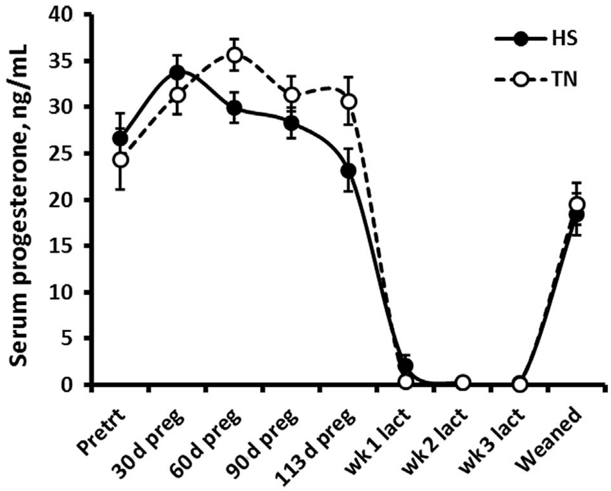

FIGURE 4 Serum progesterone concentrations in gestating first-parity sows that were either heat stressed (HS) (27–37°C; 85–55% relative humidity) or thermoneutral (TN) (15–20°C; 60–50% relative humidity) during gestation. Samples were collected pretreatment (Pretrt), during pregnancy (30, 60, and 90 days), during lactation (1, 2, and 3 weeks), or after weaning

progesterone suggests an effect of heat stress on placental progesterone synthesis, given that progesterone is synthesized by the placenta in pigs (Knight & Kukoly, 1990).

3 | LACTATION

Sows are moved to different facilities (rooms generally equipped with farrowing crates) approximately 1 week before farrowing. In most cases, farrowing rooms are cooled because sows exhibit their greatest sensitivity to heat stress during lactation (Williams et al., 2013). The subsequent sections of this review focuses on the effects of gestational heat stress on the sow after she has been moved to a thermoneutral farrowing environment.

3.1 | Thermobiology during the transition from pregnancy to lactation

A large, sustained increase in rectal temperature (1–1.5°C) was documented when the sow farrowed in either thermoneutral or heat-stress conditions (Figure 5a) (see also Gourdine, Bidanel, Noblet, & Renaudeau, 2007; Kelley & Curtis, 1978; Williams et al., 2013). Our measurements were made within environmental chambers at the University of Missouri, using first-parity sows (Lucy et al., 2012a; Williams et al., 2013). We exclusively use primiparous sows for our work in environmental chambers because they exhibit a higher risk for seasonal infertility (Bloemhof, Mathur, Knol, & van der Waaij, 2013; Gourdine et al., 2007). We also repeated the work in more typical production facilities at the University of Missouri Swine farm, with sows of mixed parities housed on conventional perforated cast iron floors (Martin, Safranski, Spiers, & Lucy, 2011; Martin, Safranski, Spiers, & Lucy, 2012). In both studies, rectal temperature was similar for primiparous and multiparous sows before farrowing, and a large increase in rectal temperature was observed in both conditions, indicating that we were not measuring an artifact associated with the environmental chambers (Figure 5). The increase in rectal temperature after farrowing, however, was greater for primiparous compared with multiparous sows in production facilities—indeed, approximately 0.4°C higher for primiparous sows during lactation, which is consistent with a previous report by Gourdine et al. (2007). Age-associated changes might reflect greater tolerance for heat production in the younger, and theoretically still-growing, sows.

An increase in rectal temperature at farrowing (Figure 5a) occurred in the absence of changes to respiration rate (Figure 5b) or skin temperature (Figure 5c), indicating that the increase in body temperature was the result of a new and higher body temperature set point, and could reflect engagement of a compensatory mechanism allowing the sow to acclimate to the increased heat production during lactation. This increase in body temperature at farrowing and lack of associated thermoregulatory response (rapid change in set point) is similar to what occurs during a fever. Indeed, an acute inflammatory

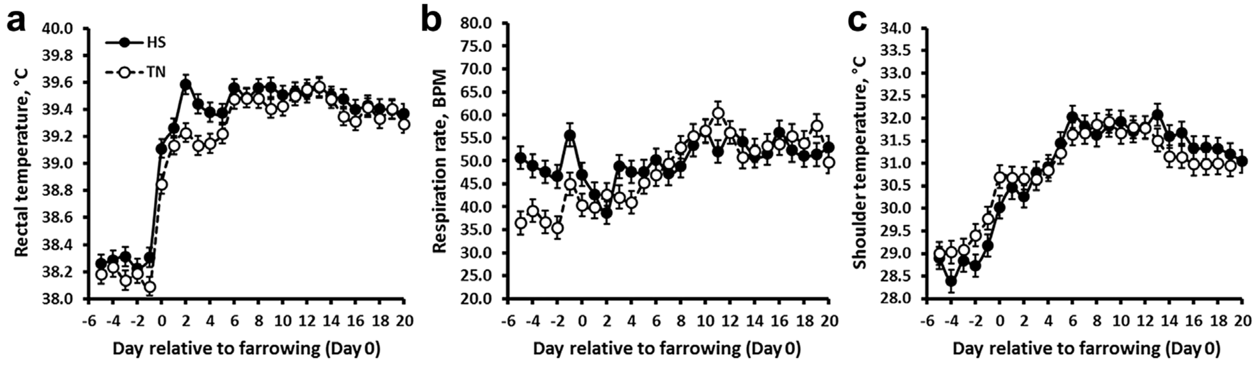

FIGURE 5 Rectal temperature (a), respiration rate (b), and shoulder temperature (c) for sows from 5 days before farrowing to 20 days after farrowing. The sows were either heat stressed (HS) (27–37°C; 85–55% relative humidity) or thermoneutral (TN) (15–20°C; 60–50% relative humidity) during gestation. Sows were moved to thermoneutral conditions within one week of farrowing, and remained in thermoneutral conditions after farrowing (Lucy et al., 2012a). BPM, breathes per minute

response at farrowing may also rapidly change the set point (Gessner et al., 2015). Temperature set points are integrated at the level of the hypothalamus (Morrison, 2016), and pyrogens can elevate the set point (Johnson Rowsey, 2013). Pyrogens, including inflammatory cytokines, may be produced throughout lactation, often arising from the involuting uterus or mobilization of adipose tissue (Vailati-Riboni et al., 2016, 2017). A higher body temperature may also reflect an increase in internal heat production after sows reach maximum feed intake approximately one week after farrowing (Williams et al., 2013).

3.2 | Carryover effects of gestational heat stress to thermobiology during lactation

Whether or not the greater initial rectal temperature during early lactation is advantageous or not is unknown. Short-term heat stress before farrowing had little effect on rectal temperature after farrowing (Williams et al., 2013), but we noted a brief period of greater rectal temperature after farrowing in sows that were heat stressed for a long period during gestation (Figure 5a) (Lucy et al., 2012a). If the increase in body temperature is a cytokine-induced, febrile response, then the larger increase in heat-stressed sows may indicate a greater inflammatory response at farrowing. Alternatively, sows that are heat stressed during gestation may have a different initial set point during lactation. Yet, this initial difference in rectal temperature was not maintained beyond the first week of lactation. Further, respiration rate (Figure 5b) and shoulder temperature (Figure 5c) after farrowing were unaffected by gestational treatment (heat stress or thermoneutral). Therefore, latent effects of gestational heat stress on the thermobiology of the sow during lactation appear to be small, based on the studies we completed (Lucy et al., 2012a; Williams et al., 2013).

3.3 | Sow endocrinology

Sows experienced large changes in metabolite and metabolic hormone concentrations during gestation, farrowing, and lactation, which were all affected by heat stress during gestation (Safranski et al., 2013).

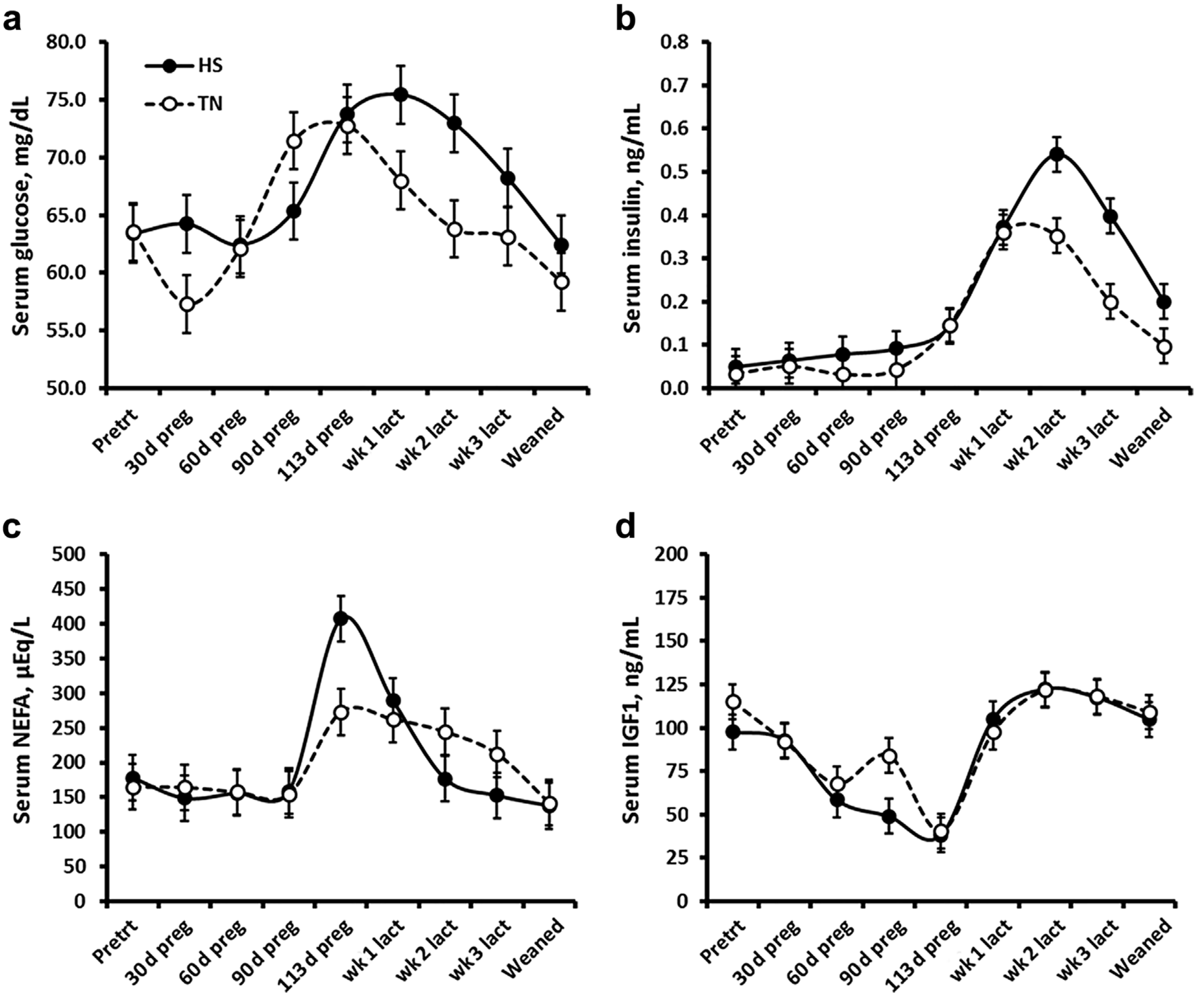

FIGURE 6 Serum glucose (a), insulin (b), NEFA (c), and IGF1 (d) in gestating first-parity sows that were either heat stressed (HS) (27–37°C; 85–55 relative humidity) or thermoneutral (TN) (15–20°C; 60–50% relative humidity) during gestation (Safranski et al., 2013). Samples were collected pretreatment (Pretrt), during pregnancy (30, 60, and 90 days), during lactation (1, 2, and 3 weeks), or after weaning

Circulating glucose concentrations in thermoneutral sows were lowest during early pregnancy, and increased at the end of pregnancy, peaking around farrowing and progressively declining during lactation (Figure 6a). Circulating insulin concentrations were suppressed during pregnancy, and did not appear to respond to circulating glucose concentrations in thermoneutral sows until after farrowing, when there was a large increase in insulin (Figure 6b). Non-esterified fatty acids (NEFA) were low during pregnancy in thermonetural sows, but increased during lactation (Figure 6c). Serum Insulin-like growth factor 1 (IGF1) concentration progressively declined during pregnancy, and then increased after farrowing in thermoneutral sows (Figure 6d). The general pattern we observed for circulating glucose, insulin, and IGF1 in the sow was similar between studies (Safranski et al., 2013; Williams et al., 2013), but differed from what was observed in the cow during the transition from pregnancy to lactation—in which glucose, insulin, and IGF1 *decrease* during lactation (Lucy, 2008). The changes in abundance of these hormones are believed to account for nutrient partitioning and NEFA release during early lactation. Sows have greater glucose, Insulin, and IGF1 levels after farrowing, but nonetheless undergo very similar changes with respect to nutrient partitioning and NEFA release as cows.

Heat stress during gestation affected the pattern of glucose, Insulin, and NEFA, but did not affect postpartum IGF1 abundance (Figure 6). Glucose (Figure 6b) and insulin (Figure 6c) concentrations were higher during lactation in sows that were heat stressed during gestation. These metrics suggest that the gestational heat-stressed sow is Insulin-resistant during lactation. NEFA release during late gestation in heat-stressed sows was also elevated (Figure 6c), which could have antagonized the action of Insulin (Luo & Liu, 2016), thus contributing to their Insulin resistance. Insulin is an important factor for follicular growth in sows, which is controlled by nutrition during lactation (Lucy, Liu, Boyd, & Bracken, 2001; Matamoros, Cox, & Moore, 1990; Quesnel, 2009). Therefore, Insulin resistance could impact rebreeding if it affects the ovary—as exemplified by chronic Insulin resistance (type 2 diabetes) in humans, which leads to a variety of life-threatening disease states (Chatterjee, Khunti, & Davies, 2017). We have not detected an effect of gestational heat stress on rebreeding performance after weaning (Williams et al., 2013), implying that the relatively short duration of Insulin resistance during lactation in gestational heat-stressed sows has fewer consequences on the ovary than pathologic Insulin resistance.

3.4 | Growth of offspring, birth to weaning

Gestational heat stress shortened the gestation period by approximately 1.5 days (115.7 ± 0.5 vs. 117.4 ± 0.5 days for heat-stressed versus thermoneutral) (Lucy et al., 2012b), but we have not consistently observed an effect of gestational heat stress on total born, born alive, still born, or number weaned metrics (Lucy et al., 2012b; Williams et al., 2013). We did not initiate full heat stress until after the fourth week of pregnancy, which may have reducd early embryonic loss, which affects total-born numbers in heat-stressed sows. Nevertheless, others reported reduced gestation length after heat stress without an effect on subsequent reproductive performance (Kattesh et al., 1980).

Gestational heat stress in ruminants decreased umbilical blood flow and umbilical uptake of nutrients and gases (Bell, McBride, Slepetis, Early, & Currie, 1989; Dreiling, Carman, & Brown, 1991). The decrease in uterine blood flow may be explained by peripheral vasodilation that shunts blood away from the abdomen (ant uterus) and towards the skin as a physiological cooling mechanism. Shunting of blood away from the uterus reduced fetal weight and birth weight gestational heat-stressed animals. In our studies, birth weight was significantly reduced for piglets born from gestational heat stress compared to thermoneutral sows (1180 ± 50 vs. 1409 ± 59 g; respectively), but weaning weights were similar, indicating the capacity of the piglets fot catch-up growth during the lactation phase (Lucy et al., 2012b). The observation that weaning weights were similar also indicated that lactation was not compromised by heat stress during gestation—in contrast to what is observed in dairy cattle, for which gestational heat stress decreased lactation yields of the dam (Tao & Dahl, 2013). In one study, sows that were heat stressed during gestation and then moved to thermoneutral conditions for farrowing had greater feed intake during lactation (Williams et al., 2013), so perhaps the catch-up growth observed previously (Lucy et al., 2012b) can be explained by greater feed intake for sows that were previously heat stressed during gestation.

3.5 | Immune function

The latent effects of gestational heat stress on immunology of porcine offspring have not been examined, to our knowledge. Dairy cows that were heat stressed during lactation, however, gave birth to calves with compromised immune function (Dahl, Tao, & Monteiro, 2016). The compromised bovine immune function began with a reduced capacity to absorb colostrum shortly after birth, although additional immune functions were deficient though weaning at 56 days of age (Tao, Monteiro, Thompson, Hayen, & Dahl, 2012). We did not observe reduced survival-to-weaning of in piglets from heat-stressed sows (Williams et al., 2013), but the possibility that gestational heat stress affects the immune function and survival of piglets to weaning, or thereafter, should be investigated further.

4 | PERFORMANCE OF OFFSPRING AFTER WEANING

Both Rutherford and coauthors (2012) and Otten, Kanitz, and Tuchscherer (2015) reviewed a variety of stressors affecting the sow during gestation that could potentially affect the fetus. They concluded that several different sow stressors—including social stress, rough handling, housing, and uterine crowding—lead to changes in developmental programming of the fetus that affected growth, behavior, the hypothalamic stress axis, and immune function of their offspring. Heat stress during gestation also appeared to affect body temperature regulation, body composition, and reproduction of offspring.

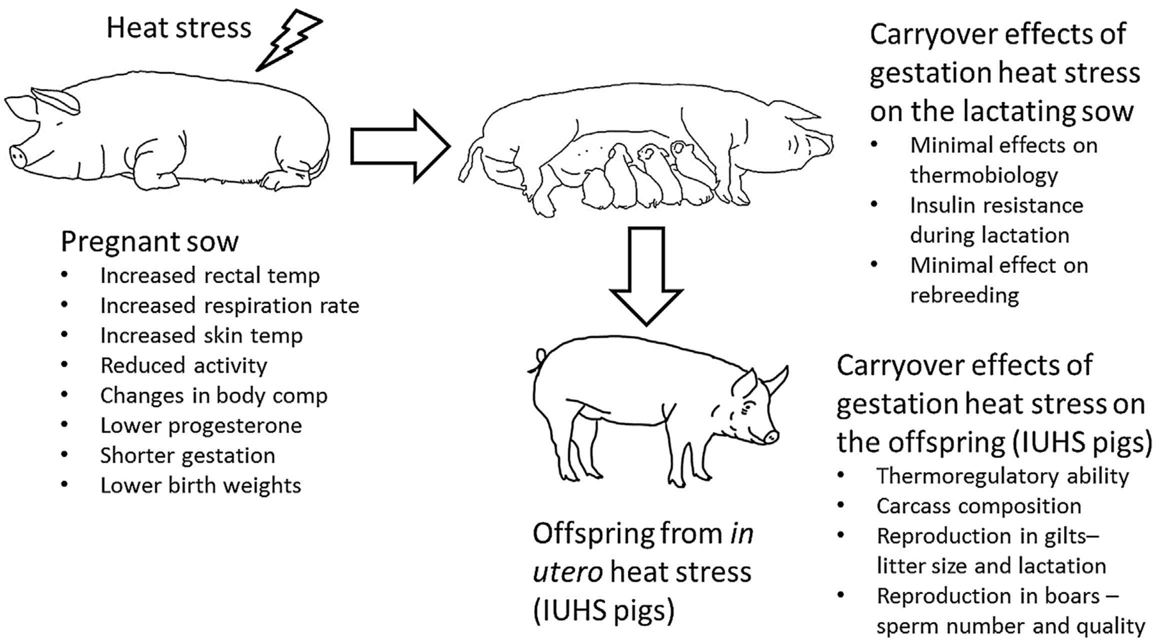

FIGURE 7 Summary of the effects of gestation heat stress on the pregnant sow and her IUHS offspring

4.1 | Body temperature regulation

Several studies examined the thermoregulation and performance beyond the lactation phase for pigs whose mothers were heat stressed during gestation. We adopted the terms "in utero heat stress" (IUHS) and "in utero thermoneutral" (IUTN) to describe gilts or boars that experienced heat stress while inside the uterus (i.e., heat stress or thermoneutral environment was applied to their mothers).

Some studies failed to detect an effect of gestational heat stress on body temperature of the offspring (Cruzen et al., 2015). Conversely, results of two studies indicated an effect of gestational heat stress on the basal body temperature in pigs (Johnson et al., 2013, 2015c; Johnson, Sanz Fernandez, Seibert, et al., 2015). For example, 8-week-old pigs challenged to two different heat-stress periods (28 to 36°C) exhibited greater body temperature for IUHS compared to IUTN pigs (Johnson, Sanz Fernandez, Seibert, et al., 2015), suggesting that gestational heat stress changed the thermoregulatory set point of IUHS offspring.

Structural or compositional differences (fat vs. lean tissue) may also affect a pig's ability to thermoregulate (Johnson, Sanz Fernandez, Gutierrez, et al., 2015; Johnson, Sanz Fernandez, Patience, et al., 2015). Indeed, Lynch and colleagues failed to detect a difference in body temperature in 3- to 6-month-old IUHS gilts compared with IUTN gilts, but did report that IUHS gilts had a lower respiration rate (Lynch, Rhoades, Lucy, & Safranski, 2014). The reduced respiration rate could indicate a greater capacity to tolerate heat-stress conditions.

4.2 | Growth and carcass composition

One significant effect of gestation heat stress may be related to the carcass composition and growth characteristics of IUHS pigs. Although catch-up growth during lactation is possible, the shift to a lighter birth weight may have long-term and measurable effects on growth after weaning (Wigmore & Stickland, 1983). Wilmoth and colleagues reported that IUHS barrows had greater feed disappearance, but reduced weight at finishing (Wilmoth, Callahan, Safranski, & Wiegand, 2015). Our data showed that IUHS and IUTN gilts housed together had similar average daily gains, but behaved differently in that IUHS gilts spent significantly more time at the feeder (Safranski et al., 2015). These unpublished data agree with those collected on littermate IUHS barrows housed individually, for which feed disappearance was significantly greater (Wilmoth et al., 2015).

Four separate studies reported differences in tissue composition between IUHS versus IUTN pigs. Two studies reported greater fat deposition in IUHS pigs (Boddicker et al., 2014; Johnson, Sanz Fernandez, Patience, et al., 2015). Other studies reported no differences for IUHS versus IUTN during the growing phase (Johnson, Sanz Fernandez, Gutierrez, et al., 2015), and an effect on head and bone development during the finishing phase (Cruzen et al., 2015). The timing of gestational heat stress and the specific experimental design of the offspring studies (including thermal treatments imposed and timing of treatments during the growth phase) may have impacted the observed results.

4.3 | Reproduction

Fetal development under heat-stress conditions damaged components of the reproductive system and compromised reproductive performance. Safranski et al. (2015) reported a numerical, albeit non-significant, reduction for first-parity IUHS versus IUTN-control gilts in terms of total born (12.06 ± 0.72 vs. 12.94 ± 0.72, respectively) and born alive (11.32 ± 0.67 vs. 11.76 ± 0.67, respectively) metrics. The difference in total born (nearly one piglet per litter) could be explained by a greater number of litters per sow, with 13–14 or 15–16 in the IUTN sows. The IUHS sows also tended to have lower piglet survival than IUTN sows, and the number weaned was one piglet fewer for the IUHS versus IUTN sows (9.91 ± 0.53 vs. 10.85 ± 0.53, respectively; not significantly different).

Gestational heat stress during a critical period of fetal ovarian development (Days 30–60 of gestation) (Black & Erickson, 1968) may reduce the total number of ovarian oocytes, thereby decreasing the capacity of each litter. Damage to the oocyte pool is likely not corrected because sows cannot regenerate oocytes after this critical period in utero. When gilts were heat stressed from weeks four to eight of gestation, and ovary weights in fetuses were measured immediately following the heat-stress treatment, no differences were found at mid-gestation (Bernhard et al., 2016), indicating that heat stress within the period for ovarian development did not affect gross measures of the ovary. Furthermore, no significant change in litter size was observed for offspring of IUHS and IUTN gilts (10.8 ± 0.8 vs. 11.6 ± 0.8, respectively) (Bernhard, Safranski, Lamberson, & Lucy, 2017), although the direction and magnitude of the numeric difference were similar to that reported by Safranski et al. (2015). Littermate IUHS boars used in the Bernhard et al. (2016) study possessed decreased sperm production and reduced sperm quality compared with IUTN boars (Proctor, Lugar, Lucy, Safranski, & Stewart, 2017). Therefore, gestational heat stress may impact the reproductive performance of both gilts and boars.

Milk composition as well as offspring of sows obtained from the Safranski et al. (2015) study were also addressed to track the long-term effects of gestational heat stress. The IUHS first-parity sows had milk with greater lactose percentage, and milk protein and solids tended to be lower from IUHS sows (Wiegert et al., 2015). Second-generation offspring of IUHS primparous sows tended to have less back fat and a longer body than IUTN-equivalent controls. The implications of these data are twofold: First, IUHS may change the biology of the lactating mammary gland, which is consistent the compromised total lactation yield of offspring from dairy cows heat stressed during late pregnancy (Monteiro, Tao, Thompson, & Dahl, 2016). Second, the effects of IUHS on offspring may persist for greater than one generation.

5 | CONCLUSIONS AND FUTURE PERSPECTIVES

Sows responded to heat stress during gestation with increased rectal temperature, respiration rate, and skin temperature (Figure 7). An additional coping mechanism was reduced physical activity, which can change body composition in favor of fatter, less-muscled sows. Heat-stressed sows exhibited shorter gestation length and reduced litter birth weight, yet lactation performance appeared normal because weaning weights were not changed when sows were heat stressed during lactation. Although gestational heat stress caused acute insulin resistance during lactation, this metabolic state did not seem to affect lactation or rebreeding performance.

Boars and gilts from sows that experienced gestational heat stress (IUHS offspring) also exhibited phenotypes related to body temperature regulation, carcass composition, and reproduction. Most of the data on IUHS pigs are preliminary, and will require further confirmation with larger sample sizes, but initial numerical differences support a negative outcome for IUHS individuals. Future studies should also examine shorter treatment periods that target specific developmental windows during gestation, given that 1- to 2-week durations mimic summertime heat waves that may acutely impact the pregnant sow, and her developing fetuses, under most agricultural settings.

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