

EFFECTS OF HEAT STRESS ON REPRODUCTION AND PRODUCTIVITY OF
PRIMIPAROUS SOWS AND THEIR PIGLETS' PERFORMANCE

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DEDICATION

This thesis is dedicated to my family and friends who have provided me with encouragement throughout the completion of my degree. I cannot accomplish my goals without your continuous support. I love you and thank you all.

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EFFECTS OF HEAT STRESS ON REPRODUCTION AND PRODUCTIVITY OF PRIMIPAROUS SOWS AND THEIR PIGLETS' PERFORMANCE

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ABSTRACT

Heat stress (HS) produces seasonal infertility in sows and decreases reproductive efficiency. The objective of this study was to examine productivity in sows exposed to HS during a production cycle (gestation, lactation, and breeding). First parity Landrace or Landrace/Large White F1 sows were rotated through environmental chambers in the Brody Environmental Center (BEC) for 55 d beginning in late gestation, continuing through farrowing/lactation and culminating in breeding. The ambient temperature sequences included either thermoneutral (TN; 18 to 20°C) or HS (24 to 30°C) for each production phase with the following treatment groups: TN-TN-TN ($n = 15$), TN-HS-TN ($n = 14$), HS-TN-HS ($n = 14$) or HS-HS-HS ($n = 15$) for gestation-farrowing-breeding (20, 24, and 11 d, respectively). Rectal temperature, respiration rate, shoulder skin temperature, body weight (BW), backfat (BF), loin eye area (LEA), feed intake (FI), metabolite concentrations, energy balance, piglet weights, follicular growth and breeding performance were measured. Rectal temperature differed across phases and conditions (38.33 and 38.22, 39.47 and 39.22, 38.79 and 38.74°C (SEM < 0.05) for HS and TN during gestation, lactation, and breeding, respectively; $P < 0.001$). Sows had similar FI (kg/d) when limit fed during gestation (2.28 ± 0.01) and breeding (1.71 ± 0.02), but

during lactation (*ad libitum*) TN sows had greater FI than HS sows (3.75 ± 0.17 vs. 3.12 ± 0.16 ; $P < 0.001$). There was no effect of treatment on BW, BF, or LEA before farrowing, after parturition and on the day of weaning. Sows in HS had less body weight gain during gestation than TN sows (11.7 ± 1.1 vs. 14.2 ± 1.1 kg, respectively; $P < 0.022$). There was an effect of treatment on the change in LEA during gestation (-2.03 ± 1.12 , -2.57 ± 1.19 , -2.68 ± 1.19 , and 1.43 ± 1.12 cm 2 for TN-TN-TN, TN-HS-TN, HS-TN-HS, and HS-HS-HS, respectively; $P < 0.050$). Sows in HS-TN-HS (-22.2 ± 3.0 kg) lost less weight during lactation (-30.4 ± 3.0 , -32.6 ± 3.0 , and -30.7 ± 3.0 kg for TN-TN-TN, TN-HS-TN and HS-HS-HS, respectively; $P < 0.084$). There was also an effect of treatment for the change in body weight and backfat depth during breeding (-11.3 ± 1.0 and -0.24 ± 0.05 , -10.0 ± 1.0 and -0.27 ± 0.05 , -10.5 ± 0.9 and -0.05 ± 0.04 , and -7.7 ± 0.9 kg and -0.07 ± 0.04 cm for TN-TN-TN, TN-HS-TN, HS-TN-HS and HS-HS-HS, respectively; $P < 0.059$). Follicular growth was affected by treatment on the day of weaning, and sows in HS-TN-HS had a greater largest follicle ($P < 0.047$). Total born (11.7 \pm 0.4 pigs), piglet birth weight (1.46 ± 0.06 kg) and total weaned (10.3 ± 0.2 pigs) were similar, but piglet weaning weight was greater at the end of lactation for TN compared with HS sows (6.21 ± 0.23 vs. 5.76 ± 0.22 kg; $P < 0.053$). Blood IGF-I was different within d 43 only (103.41 ± 8.92 , 84.83 ± 8.92 , 116.11 ± 8.92 and 89.52 ± 8.54 ng/mL for TN-TN-TN, TN-HS-TN, HS-TN-HS and HS-HS-HS, respectively; $P < 0.003$), and HS-TN-HS sows had the greatest concentrations the day before weaning (d 43). Blood NEFA concentrations were not different (153.85 ± 28.43 , 204.28 ± 23.79 , 137.02 ± 23.79 and 138.51 ± 23.79 ng/mL for TN-TN-TN, TN-HS-TN, HS-TN-HS and HS-HS-HS, respectively). Weaning to estrus interval (4.70 ± 0.12 d), percentage inseminated

sows after weaning (85.7%), subsequent farrowing rate (82.6%) and subsequent total born (10.8 ± 0.3 pigs per litter) were not different by treatment. In summary, HS decreased FI during lactation. This depression in feed intake was associated with a decrease in milk production and reduced piglet growth. There was no effect of heat stress among treatments for BW, BF, and LEA when averaged across gestation, farrowing and breeding. Heat stress, however, did impact the change in BW, BF, and LEA during the trial. Heat stress did not affect metabolite concentrations except on the day of weaning for IFG-I. Sows with greater feed intake had greater IFG-I concentrations. These sows had larger follicles at weaning, but the difference in size was not sustained. Rebreeding and second farrowing performance was not compromised by HS. To conclude, although HS increased body temperature and decreased feed intake, milk production and piglet growth, it did not detrimentally impact reproductive performance.

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CHAPTER 1

INTRODUCTION

Seasonal infertility is a common problem that occurs on commercial sow farms around the world. This phenomenon is largely caused by high ambient temperatures. High ambient temperatures cause heat stress and contribute to an increase in sow nonproductive days and compromised grow-finish performance resulting in \$299 million annual losses for U.S. swine producers (St-Pierre et al., 2003). Healthy sows not exposed to heat stress generally have short weaning-to-estrus intervals, a low incidence of anestrus and high conception and farrowing rates. Heat stress impacts these production measurements to decrease reproductive performance and lifetime productivity.

Heat stress affects sows by detrimentally affecting weaning-to-estrus intervals, the occurrence of anestrus, follicular growth, feed consumption, piglet performance and other measurements of production. Weaning-to-estrus intervals are prolonged (Messias de Braganca et al., 1998) and the incidence of anestrus increases for heat-stressed sows (Johnston et al., 1999). Typically, sows return to estrus within seven days, with primiparous sows returning within ten days. Follicular growth is one determinant of weaning-to-estrus intervals, and small follicles after weaning extend intervals to estrus and ovulation (Bracken et al., 2003). A reduction in follicular growth during lactation can be partly attributed to heat stress (Lucy et al., 2001). Also as a result of heat stress, sows

decrease feed intake to minimize heat production (Noblet et al., 1993; Messias de Braganca et al., 1998). Detrimental effects of high ambient temperature on milk production have been demonstrated, and this impact is correlated with undesirable performance of piglets (Renaudeau et al., 2001). Piglets weigh less at weaning and have a lesser growth rate when reared by heat-stressed sows (Quiniou and Noblet, 1999).

Seasonal anestrus has long been an obstacle for swine producers and many studies have been executed to elucidate the mechanisms of heat stress. The objectives of this research were to determine the thermal, metabolic, litter and reproductive responses of sows to heat stress. The purpose of this research was to determine at what phase of production the sow is most sensitive to heat stress. The information gained from this experiment will be used to recommend to producers what phase of production proves to be most beneficial to focus sow cooling efforts and change the way sows are managed during periods of expected high seasonal infertility.

CHAPTER 2

LITERATURE REVIEW

Introduction

Seasonal infertility is a common problem that occurs on commercial sow farms around the world. This phenomenon is largely caused by high ambient temperatures that affect the way in which the ovary functions. This interaction is largely determined by effects on feed intake that cause negative energy balance and weight loss. The purpose of this chapter is to review the relevant literature on reproduction in sows and the underlying mechanisms through which heat stress can affect reproduction in sows. The effects of heat stress on the growing pig will also be reviewed.

General aspects of reproduction and management of sows

Production facilities for sow management

Swine production facilities are designed for efficient flow of animals. The breeding herd typically follows a continuous cycle and moves from gestation to farrowing to breeding. More often than not, breeding and gestation barns are the same building with a separate barn for multiple farrowing rooms. These facilities are equipped

with ventilation systems that are responsible for maintaining the optimal environment for the sows. As sows move through facilities they experience changes in environments. The movement of the breeding herd begins with replacement gilts and weaned sows in the breeding barn. Weaned sows are typically housed in stalls, and replacement gilts are penned before breeding in a gestation barn. Groups of five or six gilts are typically placed into a pen with partially or fully slotted floors (Harmon et al., 2001). Gilts are moved to stalls for detection of estrus before first insemination. Sows are also inseminated in stalls, and all females remain in stalls for the majority of gestation. Stalls are placed over slotted floors (4 to 5 inches wide with 1 to 1 ¼ inch openings) or partial slats and should measure 24 inches wide by 7 feet long and 40 inches high with bars over the top to prevent sows from maneuvering out of the stalls (Harmon et al., 2001). To allow for easier insemination, stalls have an open back. A few days before expected farrowing date, sows are moved from the gestation barn into farrowing crates within specified farrowing rooms. Sows remain in the farrowing room to farrow and nurse their piglets until the day of weaning around d 21. At weaning, sows move to the breeding barn, which may be the same barn used for gestation, and piglets are moved to a nursery or wean-to-finish production facility. When sows return to the breeding/gestation barn, they are kept together in a row of stalls in order to perform estrous detection and insemination once again. This cycle is continued throughout the life of the sow.

General aspects of reproduction in sows

During lactation, follicular growth on the ovary is suppressed. A population of antral follicles is maintained during lactation that may be capable of further development after weaning in response to gonadotropin secretion (Britt et al., 1985). The secretion of

gonadotropins, luteinizing hormone (LH) and follicle stimulating hormone (FSH), are necessary for follicular growth and they bind to receptors to stimulate second messenger pathways and cause steroidogenesis in responsive cells through individual or synergistic means (Esbenshade et al., 1990). Follicle stimulating hormone initiates the growth and maturation of antral follicles during lactation into Graafian follicles (Ainsworth et al., 1990). The increase in follicle size causes an increase in estradiol concentrations as lactation progresses. Toward the end of lactation LH and FSH concentrations increase before weaning (Shaw and Foxcroft, 1985). Follicles vary in size with the average follicular population < 5 mm in diameter at weaning (Lucy et al., 2001). As the follicles grow, they become less responsive to FSH and more responsive to LH because of an increase in the number of LH receptors on follicular granulosa and theca cells (Ainsworth et al., 1990). The change in follicular FSH dependency is associated with a decrease in blood FSH (Guthrie, 2005). These follicles comprise the pool of follicles that will be selected for ovulation (Knox, 2005).

Blood estradiol increases after weaning for ovulatory sows and the increase in estradiol inhibits FSH secretion (Lucy et al., 1999). Within 6 h after weaning, an increase in LH causes development of a cohort of follicles with rapid growth (Killen et al., 1992). Concentrations of LH increase, and maximum production of estradiol is observed for 6 to 8 mm follicles at estrus (Liu et al., 2000), although the ovary may be characterized by varying sizes of follicles. Follicular populations at estrus have been estimated to consist of approximately 15 small (< 3.0 mm) and medium (3.0 to 6.9 mm) follicles and 15 large (> 7.0 mm) follicles (Knox, 2005). The LH surge causes ovulation in response to increased concentrations of blood estradiol (Ainsworth et al., 1990). The feedback actions

of estradiol act on the hypothalamus to induce the preovulatory surge of GnRH that causes the LH surge (Kraeling and Barb, 1990). At 24 h before ovulation, growth of preovulatory follicles is limited and follicle size at ovulation varies around an average of 7.1 mm (Soede et al., 1998). In response to ovulation follicles become desensitized and lose LH receptors and LH responsiveness in the follicle (Ainsworth et al., 1990). Furthermore, the production of estradiol decreases as a result of ovulation, and luteinized follicular cells begin to secrete progesterone before ovulation.

Gonadotropins (LH and FSH) and follicular growth in sows

Ovarian follicular growth is a determining factor for the return to estrus after weaning (Bracken et al., 2006a). Development of ovarian follicles is dependent partly on gonadotropins (LH and FSH). The role of LH and FSH and their receptors on follicular granulosa and theca cells is explained by the two-cell-two-gonadotropin hypothesis (Evans et al., 1981). Follicular theca cells have receptors for LH. When LH binds to its receptor, androgen is produced which diffuses into granulosa cells. As follicles develop, greater amounts of androgen are produced. Upon binding of FSH to its receptor on the granulosa cells, androgen is aromatized into estrogen. Once the production of estrogen reaches a predetermined threshold, an LH surge is initiated. Luteinizing hormone and FSH are the primary gonadotropins responsible for follicular growth and subsequent ovulation of a cohort of follicles. Follicle stimulating hormone is responsible for the early growth of the follicle until it becomes dependent on LH. Luteinizing hormone promotes further growth, maturation and ovulation.

The primary role of FSH. The primary role of FSH is to maintain antral follicle populations. An increase in blood FSH concentrations causes an increase in the number

of ovarian antral follicles (Guthrie, 2005). Follicle stimulating hormone binds to receptors on granulosa cells to promote the gradual growth of follicles up to 5 to 6 mm (Britt et al., 1985). The ovaries are characterized by a static number of predominantly small antral follicles during lactation with some of the population becoming medium-sized (< 5 mm) as lactation progresses as reviewed by Britt et al. (1985). Furthermore, FSH secretion is not as distinctly characterized by a pattern of episodic release like LH, because the secretion of LH is only partly dependent on secretion of GnRH (Britt et al., 1985). For FSH secretion, both inhibin and estradiol may be more important than GnRH (Tonetta and diZerega, 1990). Lesser blood FSH concentrations and suppressed follicular growth occurred in sows treated with charcoal extracted follicular fluid (Bracken et al., 2006a). Less FSH decreased the size of follicles and caused longer weaning-to-estrus and ovulation intervals in the treated sows. When FSH decreased, there was a delay in follicular growth 1 d after weaning with fewer follicles greater than 5 mm in diameter compared with control sows. Follicle stimulating hormone, therefore, is important for maintaining the follicle pool that partly determines when estrus occurs after weaning.

The primary role of LH. An increase in LH after weaning is necessary for final follicular growth. The control of follicular growth has been reviewed (Britt et al., 1985). The secretion of GnRH from the hypothalamus increases after weaning when the inhibitory effect of suckling is released. This causes an increase in episodic LH secretion from the anterior pituitary. The secretion of sufficient FSH and a substantial increase in episodic LH provides the stimulus for follicular growth (Varley and Foxcroft, 1990). The change in basal and mean LH concentrations after parturition and during lactation can affect subsequent return to estrus. The pulsatile release of LH during lactation averaged 3.2

pulses/12 h before weaning and increased to 7.8 pulses/12 h after weaning (Shaw and Foxcroft, 1985). Furthermore, basal concentrations and pulses of LH were increased for sows that expressed estrus within or on 4 d after weaning.

Luteinizing hormone synthesis and secretion is suppressed after parturition as a result of the inhibitory neuroendocrine reflexes acting on GnRH. Nonetheless, an increase in the amount of episodic LH secretion is observed as lactation progresses (Varley and Foxcroft, 1990). The secretion of LH is dependent on GnRH pulsatility. Sows infused with GnRH during lactation had increased serum LH concentrations concurrent with a rapid decrease in serum FSH concentrations at the beginning of infusion on d 12 after farrowing (Bracken et al., 2007). The release of LH is pulsatile with concentrations differing greatly between early postpartum and late lactation. Blood LH concentrations were high at farrowing and decreased tremendously by d 7 of lactation (Tokach et al., 1992). Furthermore, from d 7 to 28 of lactation, LH concentrations and the number of peaks increased linearly with sows with lesser LH concentrations on d 14 returning to heat later after weaning. A decrease in LH pulse frequency during lactation and a decline in basal and mean LH concentrations were associated with extended weaning-to-estrus intervals (van den Brand et al., 2000). Blood LH promotes follicular growth which partly determines weaning-to-estrus intervals.

Relationship between follicular growth and weaning-to-estrus interval

Sows returning to estrus by 3 d after weaning had larger follicles averaging 9.6 mm in diameter with ovulation occurring later after estrus than sows returning after 4 d with follicles 8.6 mm in diameter (Knox and Zas, 2001). Sows that returned to estrus sooner after weaning had larger follicles (7 mm) at d 3 after weaning (Bracken et al.,

2003) and had greater LH concentrations in the second half of lactation (Tokach et al., 1992). For large follicles to be present at weaning and weaning-to-estrus intervals to be short, LH must increase in concentration after weaning.

Sows are expected to return to estrus within 3 to 7 days after weaning (Soede and Kemp, 1997). Estrous behavior is partly dependent on follicle maturation. Growing follicles produced estrogen which initiated estrous behavior and the length of estrus varied from 24 to 96 h (Soede and Kemp, 1997). Follicular size at the onset of estrus may vary between 4 and 8 mm with follicles reaching 8 to 10 mm at time of ovulation (Waberski et al., 1999). Ovaries from ovulatory sows had follicles that increased in size from the day of weaning to d 4 and from d 4 to 6 (Langendijk et al., 2000). An LH surge must be present for follicles to ovulate with variation in the time between the peak of LH and ovulation of large follicles. Sows experienced a range of 26 to 34 h from peak LH to ovulation, with time of ovulation dependent on the length of estrus (Soede et al., 1994). Ovulation occurred 72% of the way through the duration of estrus. Intervals to ovulation from weaning and onset of estrus can be dependent on the individual sow. The weaning-to-ovulation interval varied among sows and ranged between 126 and 214 hours (Soede et al., 1994). The interval from onset of estrus to ovulation also varied and took place 10 to 85 h after estrus onset (Soede and Kemp, 1997). Ovulation of 82 and 76% of the large follicles (> 6 mm) present on the ovary occurred 48 and 72 h after weaning (Killen et al., 1992). These events describe what happens in the presence of ‘normal’ follicular growth.

Abnormal follicular growth after weaning

Sows with abnormal follicular development may become anestrous or have cystic ovaries. One reason for sows becoming anestrous may be reduced LH pulsatility.

Anestrous sows were more sensitive than ovulatory sows to the negative feedback effects of estradiol and had reduced pulsatile LH after weaning (Almond and Dial, 1990). Two types of anestrous (type I and type II) have been described for sows (Lucy et al., 2001). Type I anestrus sows have follicles 1 to 2 mm in size that do not grow during the first week after weaning. These follicles fail to develop to preovulatory size (7 to 8 mm). Type II anestrus sows have follicles that grow to 5 mm after weaning, but the follicles regress and do not reach preovulatory size. Sows do not express estrus, and their follicles do not ovulate.

Sows with cystic ovaries are characterized by follicles that have rapid growth to 20 to 30 mm in size and fail to ovulate (Lucy et al., 2001). Ovarian cysts were found in 2.36% of primiparous and multiparous sows (Castagna et al., 2004). A different study reported a higher incidence of single or multiple cysts at 30% for sows (Waberski et al., 1999). Castagna also reported that sows with cysts expressed estrus but had greater return to estrus rates (34.0%) and accounted for 10% of regular and irregular returns to estrus in this study. Cystic sows that express estrus and are inseminated may experience a decrease in farrowing rates. Farrowing rates decreased because of the presence of cysts (Waberski et al., 1999), and sows had a 52.2% adjusted farrowing rate (Castagna et al., 2004). The return to estrus interval and length of lactation may influence the occurrence of cysts. Sows with weaning-to-estrus intervals shorter than 3 d and lactation lengths shorter than 14 d had a higher incidence of cysts because of an insufficient LH surge (Castagna et al., 2004).

Follicles may grow but fail to ovulate, as observed for sows that are anestrous and have cystic ovaries. Small or medium sized follicles with or without the presence of cysts

(> 12 mm) characterized sows that failed to ovulate with estrus expression being short or intermittent (Knox and Zas, 2001). The presence of large follicles does not guarantee ovulation. Sows had extended estrus expression with large follicles (6.5 to 12 mm) that failed to ovulate according to Knox and Zas (2001).

Nutritional effects on follicular growth

Feed restriction or undernutrition can inhibit follicular growth and subsequent expression of estrus. Low dietary energy (7.88 Mcal of NE/d) feed intake caused lesser ovulation rates (16.2 ova) compared with high dietary energy with greater ovulation rates of 18.1 ova (van den Brand et al., 2000). Restricted (50% of ad-libitum) feed intake caused a decrease in mean plasma LH concentrations (Zak et al., 1997). A decrease in basal LH and FSH blood concentrations and pulse characteristics were observed in feed-restricted (70% of ad-libitum) primiparous sows that had no increase in follicular growth from d 10 (2.1 mm) to 20 (2.0 mm) during lactation (Kauffold et al., 2008). Primiparous sows that were restricted (50% ad-libitum) in feed intake had fewer LH pulses compared with sows fed close to ad libitum (Quesnel et al., 1998).

Feed intake affects ovarian and follicular characteristics. Results from Quesnel et al. (1998) demonstrated that restricted fed sows compared with ad libitum fed sows had lighter ovaries (3.1 and 3.6 g), a decrease in maximum (3.6 and 4.1 mm) and mean (2.8 and 3.3 g) follicle diameter, a decline in follicular volume (15 and 19 mL) and fewer follicles greater than 4 mm (0.2 and 2.5) at weaning. The frequency of LH pulses was lower for these sows, and this may have been part of the reason for the observed changes in the follicles and ovaries. Follicle diameter is lesser for sows with low feed intake or changes to the diet. Sows fed at a low level had follicles 3.0 mm in size 2 d after

weaning that were smaller than those that were fed at a high level that had follicles 3.8 mm in size (van den Brand et al., 2000). Furthermore, sows with a higher loss of protein during lactation had fewer follicles greater than 4 mm (23.6%) in diameter compared with sows with less protein loss (55.4%) at weaning (Clowes et al., 2003). Bracken et al. (2003) reported that sows with low body condition scores had small diameter follicular populations on d 3 after weaning. Sows restricted in feed intake have smaller ovaries and smaller follicles at weaning.

Metabolite effects on follicular growth

Follicular development may be modified metabolically when nutrition is restricted. Nutrition affects blood IGF-I, GH and insulin concentrations, which have subsequent consequences on reproduction and follicular development during lactation. During lactation IGF-I and GH increase, while there is inconsistency in whether insulin concentrations decrease or increase (Lucy, 2008). The increase in IGF-I and GH are coupled during early lactation, and it has been suggested that the increase in GH combined with *ad libitum* feeding promote liver production of IGF-I as reviewed by Lucy (2008). Furthermore, IGF-I concentrations may decrease over time and become uncoupled from GH in late lactation because the sow may become catabolic.

The important role of IGFs has been reviewed. Follicular granulosa cell function is dependent on IGFs for cell replication and differentiation and the stimulation of LH receptor induction (Tonetta and diZerega, 1990). A positive correlation was also observed for plasma IGF-I concentrations on the day of weaning and LH pulsatility and the LH surge. Insulin-like growth factor-I and the type I IGF receptor are important in hormone action. The amount of IGF-I is correlated with follicle size, day of follicular

phase and estradiol concentrations (Hammond et al., 1993). Granulosa and theca externa cells were found to have IGF-I mRNA. The type I IGF receptor mRNA was expressed on granulosa cells in 2 to 8 mm follicles (Liu et al., 2000) indicating that IGF-I and its receptor are necessary at each stage of follicular growth.

Nutritional restrictions reduce the concentrations of IGF-I and insulin in the blood (Lucy, 2008). Plasma IGF-I concentrations were lesser for sows that weighed less at parturition and had increased body weight loss during lactation with a decrease observed at weaning for all sows (van den Brand et al., 2001). A review on follicular development indicated that undernourished sows had decreased plasma IGF-I and insulin concentrations that decreased the response of the ovary to LH (Hunter et al., 2004). This resulted in decreased follicular growth.

Concentrations of insulin and IGF-I were determined to be positively correlated in lactating sows (van den Brand et al., 2001). Insulin promoted an increase in IGF-I production to mediate follicular growth (Cox, 1997). By mediating follicular growth, these metabolites affect weaning-to-estrus intervals. Insulin concentrations were greater d 7 of lactation for sows that had weaning-to-estrus intervals of less than 9 d (Tokach et al., 1992). Furthermore, insulin concentrations were correlated with the number of LH peaks. Insulin and IGF-I are synergistic with gonadotropins to stimulate ovarian follicular growth and steroidogenesis (Lucy, 2008).

Other factors that affect weaning-to-estrus interval

Ovulation may be influenced by lactation length and weaning-to-estrus interval. Sows that lactated for longer than 16 d or that return to estrus four or more days after

weaning are more likely to ovulate than sows that lactate for fewer days and return to estrus sooner (Knox and Zas, 2001).

Reproductive performance can vary depending on genetics and parity. Sows selected for ovulation rate and uterine growth were compared with controls to assess reproductive performance (Freking et al., 2007). Ovulation rate was greater for sows selected for ovulation rate (18.0 ova) than the controls (15.0 ova) or those selected for uterine growth (14.0 ova). High ovulation rate sows, however, had the greatest embryonic mortality rate before d 45 of gestation. Fetal and placental weights were greater for control and uterine growth sows by d 85 of gestation compared with sows selected for ovulation rate.

Environmental factors, such as heat stress, have an impact on sows with variation in reproductive performance observed for different genetic lines. In thermoneutral environments, a Dutch purebred Yorkshire line had a greater farrowing rate, larger litter size and greater total number born than an International purebred Large White line (Bloemhof et al., 2008). When temperatures rose above 25°C, however, the Large White sows had greater farrowing rates and total number born than the Yorkshire sows. Reproductive performance was compared for multiparous Large White and Creole breeds in a hot tropical climate (Gourdine et al., 2006a). Large White sows had more pigs born alive at 10.9 pigs compared with 10.1 pigs born alive for the Creole sows. When the number of still born were compared, however, Large White sows had 9.1% still born compared with 3.6% still born for Creole sows.

Reproductive performance is also influenced by parity. Parity affected ovulation rate with primiparous sows having 14.7 corpora lutea and second and third parity sows

having 17.1 and 21.4 corpora lutea, respectively (Killen et al., 1992). Primiparous sows experienced a greater rate of infertility (33.4%), or not returning to estrus within 14 d of weaning, following their first lactation compared with subsequent lactations (17.6%) (Maclean, 1969). Heat stress has greater implications on primiparous sow reproductive performance than on multiparous sows. Primiparous sows had longer weaning-to-estrus intervals (11.0 d) and fewer sows came into estrus within 7 d (80.6%) during the spring and summer months compared with multiparous sows (5.7 d; 92.8%) (Clark et al., 1986).

Heat stress and sows

Effects of heat stress on physiological response

Heat stress invokes physiological responses from sows. The physiological responses include increases in respiration rate and body and skin temperatures. Respiration rate is greater and skin temperature is greater because of an increase in peripheral blood in an effort to increase heat loss to the environment. Physiological responses to heat stress may depend on phase of production and reproductive status of the sow. An early study determined that the respiration rate of a late pregnant sow was 186 bpm whereas, an open sow had a respiration rate of 64 bpm in the same ambient temperature of 36.7°C (Heitman et al., 1951). This study indicates that gestating sows have greater metabolic heat production. The ability of sows to dissipate heat is partly dependent on respiration rate, as the increase in respiration rate is a cooling mechanism used by sows. An increase in skin temperatures also demonstrates an attempt to dissipate heat through vasodilation. Sows redirect blood flow from other tissues and organs to the

skin for heat dissipation (Black et al., 1993) and their skin temperature increases when they do this.

Early and late gestating sows respond to heat stress by increasing rectal temperature and respiration rate. Average rectal temperatures were greater for gestating gilts in a heat-stressed environment (37.8°C , 17 h; 32.2°C , 7 h) than control gilts (23.3°C) (Omtvedt et al., 1971). Early gestating gilts exposed to a constant (33°C) or cyclic (25°C , 6 h; 34°C , 3 h; 25°C , 15 h) heat stress from d 3 to 30 of gestation had an average rectal temperature of 39.1°C and respiration rate of 58.9 bpm compared with 38.8°C and 25.9 bpm for sows in a constant thermoneutral environment of 23°C (Liao and Veum, 1994). Thermal responses to heat stress are also observed in late gestation. Late gestating sows exposed to 32°C had a greater rectal temperature of 39.6°C and a greater respiration rate of 97.7 bpm than thermoneutral (21°C) sows with a rectal temperature of 39.0°C and a respiration rate of 36.0 bpm (Machado-Neto et al., 1987).

Lactation has an effect on rectal temperatures and sow heat abatement. Rectal temperatures tend to increase around the time of parturition and stay elevated during lactation because of an increase in metabolic heat production. Rectal temperatures around parturition and during lactation were greater for multiparous and primiparous sows exposed to 30°C compared with 20°C (Prunier et al., 1997). Lactating primiparous sows that were heat-stressed (30°C) had greater rectal temperatures than control (20°C) sows, while all sows had greater rectal temperatures after parturition than before farrowing (Messias de Braganca et al., 1998). In one study, however, respiration rates and rectal temperatures were greater before and during parturition for sows and gilts exposed to heat stress (29.8 vs. 20.5°C for thermoneutral) whereas there were no differences seen

postpartum (Kelley and Curtis, 1978). An increase in respiration rate has been reported in heat-stressed sows during lactation. Sows initially increased respiration rates to adapt to heat stress but were capable of adjusting to high temperatures resulting in slightly reduced respiration rates after d 10 to 20 of lactation (Johnston et al., 1999). In agreement with the previous study, respiration rate and rectal temperature were greater in heat-stressed sows, and heat-stressed sows had the capacity to adapt to the environment with respiration rates declining throughout lactation (Schoenherr et al., 1989; Spencer et al., 2003).

Rectal temperatures are related to skin temperatures with a narrow range in temperature difference during heat stress. The difference between rectal and back and rectal and flank body temperatures decreased when ambient temperatures were at or above 27°C (Quiniou and Noblet, 1999). Multiparous lactating sows had greater average skin and rectal temperatures of 37.4°C and 39.4°C when exposed to 29°C compared with sows exposed to 18°C that had average temperatures of 34.6°C and 38.6°C for skin and rectal temperatures, respectively (Quiniou and Noblet, 1999). Skin temperature was 36.3°C and rectal temperature was 38.9°C for heat-stressed (28°C) multiparous lactating sows compared with 33.0°C and 38.4°C for control (20°C) sows for skin and rectal temperatures, respectively (Renaudeau et al., 2003b).

As a result of weaning, there is less metabolic demand on the sow and this may affect skin and body temperatures. After weaning, skin and rectal temperatures decreased for multiparous sows with less of a decrease observed for skin temperatures for sows exposed to 29°C compared with 20°C (Renaudeau et al., 2001).

Effects of heat stress on the follicle

Heat stress has deleterious effects on follicular growth. Typical follicular populations during lactation consist of small and medium sized follicles less than 5 mm in size. Follicles grow to greater than 8 mm after weaning (Britt et al., 1985). Follicular populations at weaning for thermoneutral sows consisted of follicles that were 4 to 5 mm in diameter (Lucy et al., 2001). On the other hand, heat-stressed sows had ovaries with no follicles 4 to 5 mm in size and were characterized by follicles < 2 to 3 mm. After weaning, follicular growth for thermoneutral sows occurred rapidly with follicles reaching 8 mm. Heat-stressed sows had 4 to 5 mm follicles at 4 d after weaning. The delay in follicular growth prolonged return to estrus for heat-stressed sows (Lucy et al., 2001). Anestrous sows had ovaries with follicles < 5 mm in diameter with no corpora lutea when ovariectomies were performed 45 d after weaning (Almond and Dial, 1990).

Effects of heat stress on weaning-to-estrus interval

Heat stress causes anestrus and prolonged weaning-to-estrus intervals in sows. Fewer heat-stressed (27°C) sows returned to estrus 10 d after weaning at 38.9% compared with 76.5% of the thermoneutral (18°C) sows (Prunier et al., 1997). Also, sows that farrowed in the warm season (May through October) returned to estrus 5.08 d after weaning compared with 4.38 d for cool season (November through April) sows (Dove and Haydon, 1994). Sows weaned in the spring and summer had longer return to estrus intervals of 8.0 d when compared with sows that returned in 6.0 d after weaning in the fall and winter months (Clark et al., 1986). Furthermore, this study determined that the percentage of primiparous sows inseminated within 7 d was less at 80.6% compared with

92.8% of multiparous sows. Primiparous sows also had weaning-to-estrus intervals that were 8 d longer in the summer compared with the winter (Cox et al., 1983).

Bracken et al. (2003) reported that longer intervals to estrus and ovulation are typically associated with first parity sows. The occurrence of anestrus and the number of primiparous sows that return to estrus after breeding were greater with each incremental increase in temperature (Teague et al., 1968). The effects of heat stress on the increase in weaning-to-estrus intervals may be compounded with other variables, such as sow body condition. Bracken et al. (2003) found an increase in intervals to estrus to be especially evident for primiparous sows with low body condition scores. Sows with body condition scores of one (thin) had a weaning-to-estrus interval of 9.4 d, and sows with scores of two or three to four had weaning-to-estrus intervals of 7.1 and 8.1 d, respectively.

Sows that do not have prolonged weaning-to-estrus intervals during heat stress may nonetheless exhibit irregular returns to estrus. During the months of August through November in Finland, the rate of irregular returns to estrus increased as a result of heat stress (Peltoniemi et al., 1999). Johnston et al. (1999) did not observe an effect of heat stress during lactation on weaning-to-estrus intervals, but did find a lower proportion of heat-stressed sows expressed estrus by d 15 after weaning.

Weaning-to-estrus intervals consequently affect intervals to insemination and conception. Tantasuparuk et al. (2000) reported that weaning-to-insemination interval increased by 0.17 day with each 1°C increase at the maximum daily temperature for multiparous sows. Weaning-to-insemination (Almond and Bilkei, 2005) and weaning-to-conception intervals were prolonged during heat stress, with younger sows more affected than older sows (Tantasuparuk et al., 2000). Primiparous sows with longer weaning-to-

ovulation intervals (10.6 d) had a decreased conception rate of 63% compared with second (87%) and third or greater (81%) parity sows with weaning-to-ovulation intervals of 9.2 and 7.6 d, respectively (Bracken et al., 2003).

Conversely, no differences were found in weaning-to-estrus intervals for heat-stressed sows. Weaning-to-estrus intervals were variable and were not different between sows that were restricted or ad libitum fed in a thermoneutral (20°C) environment (Messias de Braganca et al., 1998). In a different study, weaning-to-estrus intervals were not different for sows among the four seasons (Stansbury et al., 1987). Within this study, a second experiment determined that sows in the thermoneutral environment at 18°C actually had a longer weaning-to-estrus interval of 7.3 d when compared to 4.4 or 5.3 d for sows in farrowing rooms with higher temperatures of 25 and 30°C, respectively, when snout coolers were used on all sows. The effect floor type has on promoting heat loss was also evaluated. This may be one reason for why the sows in the heat-stressed environment had shorter weaning-to-estrus intervals.

Use of P.G. 600 to treat anestrous sows during heat stress

A higher incidence of anestrus and extended weaning-to-estrus intervals increase sow non-productive days and negatively affect sow lifetime productivity. Non-productive days encompass all days the sow is not gestating or lactating. Collectively these effects have a major impact on farm profitability. One way estrus can be induced in seasonally anestrous sows is by administration of P.G. 600®, a combination of equine (400 IU per mL) and human (200 IU per mL) chorionic gonadotropins. Sows treated with P.G. 600® at d 7 after weaning had larger follicles with average diameters of 4.8, 5.2, and 5.4 mm compared with 3.6, 4.4, and 4.0 mm for saline control sows in groups one, two and three,

respectively (Bracken et al., 2006b). A greater number of P.G. 600[®] sows than control sows expressed estrus (93 and 32%), ovulated (72 and 11%), were inseminated (90 and 29%) and became pregnant (79 and 18%). First and second parity sows treated with P.G. 600[®] at weaning expressed estrus sooner at 6.0 and 4.8 d compared with weaning-to-estrus intervals of 7.8 and 6.4 d for untreated first and second parity sows, respectively (Bates et al., 1991). There were no differences in weaning-to-estrus intervals for parity three and older sows. Fewer parity one sows treated with P.G. 600[®] (15.6%) were anestrous than controls (29.2%), and no differences were observed in older parities. This study also examined the effects of P.G. 600[®] on number born alive. Sows treated with P.G. 600[®] had fewer born alive across parities than control sows at 10.10 and 10.55, respectively. Although there were differences in born alive, fewer sows were anestrous and weaning-to-estrus intervals were shorter indicating that P.G. 600 may still be a useful tool. In a different study, no differences were seen in total number born (10.6 and 11.9) or farrowing rate (71.1 and 67.4%) for P.G. 600[®] treated and control mixed parity sows, respectively (Knox et al., 2001). Sows returned to estrus by 3.8 d, and 94.4% expressed estrus within 8 d for P.G. 600 sows which was different than 4.9 d and 78.4% for control sows. As evidenced by these studies, P.G. 600[®] may be an effective method to induce estrus and shorten weaning-to-estrus intervals in weaned sows.

Effects of heat stress on gonadotropins

Blood LH concentrations and LH pulse frequency and amplitude are reduced when sows are heat-stressed. Lesser concentrations of serum LH were noted in anestrous sows in the summer as a result of lesser hypothalamic GnRH concentrations (Love et al., 1993). Also, blood LH concentrations were depressed during exposure to heat stress

(Barb et al., 1991; van den Brand et al., 2000). Furthermore, the LH pulse frequency was greater in thermoneutral sows compared with heat-stressed sows, whereas pulse amplitude was less (Barb et al., 1991). Luteinizing hormone secretion, therefore, is reduced by heat stress during lactation. Lesser LH promotes extended weaning-to-estrus intervals because follicles depend on LH for maturation to preovulatory size.

Embryonic loss and farrowing rates in heat-stressed sows

Heat stress decreases reproductive performance by having an impact on embryo mortality and viability. Sows that were heat-stressed (40.2°C) during early gestation, on d 2 through 13, had greater embryonic mortality of 63% and lesser litter sizes of 4.9 fetuses than control (24.0°C) sows with 35% embryonic mortality and 8.8 fetuses (Wildt et al., 1975). This study also reported no differences in embryonic mortality or litter size when sows were heat-stressed (40.4°C) on d 14 through 25 of pregnancy compared with controls (23.3°C). Wildt et al. (1975) determined that in both heat-stressed groups (d 2 through 13 and d 14 through 25), 68.4% of fetuses were degenerating at d 42 of pregnancy, which was greater than 38.9% for control sows. Five pregnant primiparous sows were heat-stressed for 12 h at 37°C and 12 h at 32°C from d 8 to 16 after estrus onset, and two sows had fragmenting embryos at d 16 (Wettemann et al., 1988). Embryos from heat-stressed sows had an average wet weight of 233 mg, whereas embryos from control sows exposed to 21°C weighed 366 mg. When sows were exposed to heat stress (35°C) for 48 h on d 1 or 20 of gestation and compared with controls (15.5°C), there was a 4.1% decrease in the number of viable embryos for d 1 heat-stressed sows and a 13.6% decrease in the number of viable embryos for d 20 heat-stressed sows (Tompkins et al., 1967). Furthermore, sows were heat-stressed (36.7°C) on d 1 through 5 or d 20 though

25 of gestation (Tompkins et al., 1967). This study reported 12.2 viable embryos for sows heat-stressed later in gestation which was greater than 6.8 viable embryos for sows heat-stressed earlier in gestation.

Primiparous sows that were heat-stressed (32.2°C) from d 3 to 25 postbreeding had 11.3 embryos, which was less than sows in the thermoneutral (15.5°C) environment that had 13.6 embryos (Warnick et al., 1965). This study also reported no differences in embryo survival for up to 3 d postbreeding. The period of placentation is sensitive to heat stress, and an increase in embryonic loss occurs as a result of heat stress. Gilts exposed to heat stress (37.8°C , 17 h; 32.2°C , 7 h) during d 8 to 16 of gestation had 5.9 fewer viable embryos than control (23.3°C) gilts (Omtvedt et al., 1971). Heat stress was also analyzed postbreeding with gilts heat-stressed from d 1 to 15 of gestation having fewer viable embryos (8.7) than gilts heat-stressed from d 15 to 30 (12.5) or not heat-stressed (12.2) at all (Edwards et al., 1968). The effect of heat stress on breeding was analyzed, and no differences were observed in conception rates for gilts in the hot chamber (38.9°C , 17 h; 32.2°C , 7 h) compared with the cool (23.4°C) chamber (Edwards et al., 1968). In a different study, conception rates were not affected by heat stress (32.2°C), but three of thirteen gilts ovulated without estrus (Warnick et al., 1965). A review of the literature concluded that heat stress beginning the day of mating through d 16 of pregnancy resulted in a decrease in conception rates and a reduction in litter size with a decrease in embryonic tissue by d 16 (Wettemann and Bazer, 1985).

Early embryonic loss resulting from heat stress impacts farrowing rates and results in a lower number of piglets born. Total born and born alive were negatively correlated with high temperature and humidity during the first 5 weeks of gestation

(Tummaruk et al., 2004). The same study reported that lesser litter size was found in heat-stressed sows, with the effect of farrowing month being most pronounced in first parity sows. When maximum temperatures increased by 1°C during the first four weeks of gestation, total born decreased by 0.07 pigs per litter (Tantasuparuk et al., 2000). Farrowing rates and litter size decreased for sows exposed to > 35°C compared with sows exposed to < 30°C during each summer from 1998 to 2003 (Almond and Bilkei, 2005). In Thailand, farrowing rate decreased and born alive decreased for sows that were mated during the hot and rainy season (Tantasuparuk et al., 2000). The greatest number of sows failed to farrow when inseminated during July and August with approximately 29% of inseminations not resulting in farrowing (Stork, 1979). Furthermore, a decreased farrowing rate of 63% was partly attributed to early embryonic loss during summer months (Tast et al., 2002).

The effects of heat stress were also evident during late gestation, resulting in an increase in the number of still born. Omtvedt el al. (1971) reported an increase in the incidence of still born in first parity sows heat-stressed (37.8°C, 17 h; 32.2°C, 7 h) during late pregnancy (102 to 110 d) compared with control sows. Heat-stressed sows had 5.2 still born compared with 0.4 still born for control sows. Heat-stressed sows during late pregnancy had fewer piglets born alive with an average of 6.0 compared with control sows that averaged 10.4 pigs born alive. The greatest loss in productivity was seen at this stage of gestation, and no differences were observed earlier in gestation (53 to 61 d). Furthermore, in a different study, there were fewer still born for warm (1.1) compared with hot (2.0) season sows (Renaudeau et al., 2003a).

The collective interpretation of the data is that embryonic survival, farrowing rates, litter sizes and still born are negatively impacted by heat stress. Liao and Veum (1994), however, did not observe a decrease in embryo survival from d 3 to 24 or 30 of gestation when primiparous sows were exposed to cyclical heat stress (25°C, 6 h; 34°C, 3 h; 25°C, 15 h) or a constant temperature (32°C). These sows may not have been exposed to heat stress for a long enough time period during the cyclic heat stress or the constant heat stress temperature may not have been high enough to decrease embryo survival.

Effect of heat stress on feed intake, energy balance and milk production

Sow milk production. Milk production is dependent on mammary blood flow and nutrient availability. In heat-stressed sows (30 and 29°C; respectively), more adipose tissue (Barb et al., 1991) and protein (Quiniou and Noblet, 1999) were mobilized in an effort to produce more milk. Decreased nutrient availability as a result of decreased feed intake in heat-stressed sows detrimentally affects milk production. The decrease in milk production in heat-stressed sows may affect litter growth. Sows that ate less during the hot season (average 26.1°C) produced less milk and had reduced litter growth (Silva et al., 2009) than during the warm season (average 23.6°C). Detrimental effects on milk production were also seen for sows exposed to 29°C who produced less milk compared with sows at 20°C over a 28 d lactation (Renaudeau et al., 2002). No differences in milk production were noted between heat-stressed (32°C) and thermoneutral (20°C) sows in one study (Schoenherr et al., 1989). In that study, Schoenherr et al. (1989) reported that milk production decreased initially, but as lactation progressed it increased linearly for heat-stressed sows as a result of adaptation to their environment. Milk production reached a plateau by d 13 to 17 for thermoneutral sows (Schoenherr et al., 1989). In agreement

with the previous study, Barb et al. (1991) demonstrated similarities in milk production and litter weights for sows exposed to 22 or 30°C.

Milk production is dependent on feed consumption and diet in lactating sows. Sows fed a diet that was high (14.2 Mcal of ME/d) in energy reached maximum milk production by d 21, whereas sows fed a low (10.4 Mcal of ME/d) energy diet had a plateau in milk production by d 17 of lactation (Noblet and Etienne, 1986). Dietary protein was manipulated in one study in an effort to alleviate the negative effects of high ambient temperature (29°C) on milk production and piglet performance (Renaudeau and Noblet, 2001). In that study, the dietary changes did not lessen the unfavorable effects of heat stress. According to Renaudeau et al. (2003a), an increase in dietary fiber (decrease in energy intake) increased lean tissue mobilization, and milk production was maintained to result in increased litter weight gain even though sows were energy restricted.

Milk synthesis is also dependent on mammary blood flow and mammary blood flow changes in response to heat stress. After a sow eats, mammary blood flow decreases but then increases with time to the level observed before eating (Renaudeau et al., 2002). The decrease in level is partly attributed to sows standing up and redistributing blood flow to the digestive tract. Heat-stressed sows require a greater amount of blood flow to the mammary gland to produce 1 kg of milk compared with thermoneutral sows. This may be attributed to an increase in the amount of blood occupying skin capillaries to dissipate heat and may lead to lesser efficiency for the mammary gland (Renaudeau et al., 2003b). An additional observation from Renaudeau et al. (2003b) was that heat-stressed sows spent less time standing. Sows that spend less time standing may consume less feed.

Fewer nutrients, therefore, are available for milk synthesis even though there is an increase in blood flow to the mammary gland while sows are lying down.

Milk availability affects nursing behavior. Renaudeau and Noblet (2001) reported that suckling frequency (39.2 vs. 34.2 times/d) was greater, and suckling intervals (37.0 vs. 42.4 min) were shorter at 29°C than at 20°C. In another study, piglets nursed 40 times/d during lactation when sows were exposed to an ambient temperature of 29°C compared with 26 times/d at 18°C (Quiniou and Noblet, 1999). These observations indicate that piglet nursing behavior may be dependent on the availability of milk. In the study by Renaudeau and Noblet (2001), piglets from heat-stressed sows nursed more often in an attempt to meet their nutrient requirements. These piglets theoretically expended more energy with no additional energy intake. This phenomenon may have contributed to decreased growth performance of piglets.

Heat-stressed sows have a reduction in milk production that can be partly explained by a decrease in feed intake. Thermal responses to heat stress and piglet behavior during heat stress can also contribute to a decrease in milk production (King, 2000). Collectively, the studies indicate that milk production is primarily dependent on the ability of the sow to consume enough feed to provide nutrients for milk synthesis. Heat stress affects feed intake, mammary blood flow, and nursing behavior. These effects have repercussions in terms of milk production and piglet growth.

Sow energetics (Energy Balance). Metabolizable energy (ME) in feed is composed of net energy (NE) and the heat increment for digestion and metabolism. Sows used 77.4% of ME for NE. Digestive and metabolic heat production accounted for the remaining 22.6% of ME (Noblet et al., 1993). Sow energy intake was used for fasting heat production,

thermic effect of food and physical activity and accounted for 75.6% of total heat production (Noblet et al., 1993). Feces, urine and methane production used 15.3, 5.3, and 1.1%, respectively, of energy intake. Sows were fed at their maintenance level and had a positive energy balance and this accounted for the remaining 2.6% of energy.

Energy requirements are different during gestation and lactation. Daily maintenance requirements in thermoneutral environments for gestating and lactating sows are 105 and 110 kcal ME/kg BW^{.75}, respectively (Noblet et al., 1990). Sows that do not consume enough ME to meet maintenance and lactation requirements have decreased performance during lactation. Diets formulated to provide a low energy of 104 kcal ME/kg BW^{.75}/d to sows resulted in depressed milk production and an increase in lipid mobilization in order to provide the energy needed to produce milk (Noblet and Etienne, 1986).

Lactating sows are in a negative energy balance after farrowing. Negative energy balance is caused by an increase in energy demand because of lactation and the inability of the sow to consume enough nutrients to meet the energy demands (Noblet et al., 1990). Energy balance was calculated according to the formula by Noblet et. al (1990): $EB_{lact} = [FI \times ED - (22.0 \times BW + 6.83 \times LG - 125 \times n + 1430)]/1,000$ where EB = energy balance during lactation (Mcal of ME/d), FI = feed intake (kg), ED = feed energy density (kcal of ME/kg), BW = mean sow body weight, LG = litter body weight gain, and n = number of pigs in the litter and converted to Mcal of ME/d (Willis et al., 2003).

A negative energy balance is characteristic of lactating sows because they mobilize body reserves and have increased weight loss (Noblet et al., 1990). Regardless of ambient temperature, energy balance is negative after parturition. Primiparous sows

that lactated for an average of 25 d in a thermoneutral environment had a negative energy balance at weaning (Willis et al., 2003). Negative energy balance is largely associated with inadequate feed intake. Low feed intake contributed to a negative energy balance in lactating primiparous sows that were not heat-stressed (van den Brand et al., 2000). If energy balance, therefore, is already negative for lactating sows, then heat stress may further exacerbate this effect through a decrease in feed intake. Greater negative energy balance because of a decrease in feed intake may suppress LH secretion and follicular growth and may, in turn, increase anestrus in heat-stressed sows.

Sow feed intake and body weight loss. Heat-stressed sows decrease feed intake in an effort to reduce heat production. The decrease in feed intake is especially evident during lactation when sows are attempting to reduce body heat production. The decline in feed intake has detrimental effects on sow body weight and body condition. A negative impact on feed intake and a decline in body weight gain was observed for sows exposed to high temperature (33.3°C) when compared with sows exposed to a lower temperature (26.7°C) during breeding and early gestation (Teague et al., 1968). Heat-stressed sows consumed 1.69 kg/d with an average daily gain of 0.28 kg compared with feed consumption of 2.15 kg/d with an average daily gain of 0.51 kg for sows in a lower temperature. Several studies have determined that sows exposed to heat stress consumed less feed than thermoneutral sows during lactation. During the warm season (May through October), sows consumed 3.9 kg/d during 21 d of lactation compared with cool season (November through April) sows that consumed 4.9 kg/d (Dove and Haydon, 1994). Multiparous lactating sows were exposed to 18, 22, 25, 27 or 29°C for 21 d (Quiniou and Noblet, 1999). Feed intake was the least for sows at 29°C with sows consuming 3.1 kg/d. The

greatest intake was observed at 18 (5.7 kg/d) and 22°C (5.4 kg/d). Heat-stressed (29°C) multiparous sows consumed less feed compared with thermoneutral (20°C) sows for the duration of lactation (Renaudeau et al., 2001). Primiparous sows were used in the following study that determined that heat-stressed (32°C) sows had decreased feed intake at 4.6 kg/d compared with thermoneutral (21°C) sows with feed intake of 7.5 kg/d (Spencer et al., 2003). Multiparous and primiparous sows were heat-stressed at 27 and 30°C, respectively, and feed intake was compared with thermoneutral (18 and 20°C, respectively) sows (Prunier et al., 1997). Heat-stressed sows consumed less at 4.4 and 2.7 kg/d compared with 6.1 and 3.0 kg/d for multiparous and primiparous sows, respectively.

Heat-stressed sows had a decline in feed intake by 13%, resulting in greater body weight loss during lactation (McGlone et al., 1988b). In a second study, feed intake was reduced by 43% for lactating sows in a high constant temperature with greater body weight loss and lesser body reserve mobilization than thermoneutral sows (Messias de Braganca et al., 1998). Heat-stressed sows exposed to 29°C lost up to 36 kg of body weight, which was greater than lactating sows at 18, 22, and 25°C (Quiniou and Noblet, 1999). Sows consumed 462 g/d less and 584 g/d less feed with each 1°C increase in ambient temperature according to the work of Silva et al. (2009) and Renaudeau et al. (2003a), respectively. In tropical climates, sows are exposed to warm and hot seasons with ranges in temperature and humidity that affect body weight loss and feed intake. Sows in tropical climates experience a warm season (average 25°C; range 21.7 to 29.9°C) and a hot season (average 27.5°C; range 24.0 to 32.3°C). Renaudeau et al. (2003a)

confirmed that sows have a reduced feed intake and greater body weight loss during the hot season.

Gourdine et al. (2006a) reinforced previous findings when Creole and Large White sows were studied during a 29-d lactation in a tropical climate. Both breeds exhibited a decrease in feed intake and an increase in body weight loss during the hot season. In a related study, heat-stressed Large White sows consumed an average of 3.9 kg/d from farrowing to weaning, while control sows consumed 5.0 kg/d (Gourdine et al., 2006b). The decrease in feed intake for the heat-stressed sows was explained by a reduction in feed intake during the day rather than during the night. During the night, meal size and rate of intake decreased for Creole sows in this trial, whereas more than half the feed intake was consumed during nighttime hours for the Large White sows. The number of meals was not different, but the length of time sows ate was less during heat stress (Gourdine et al., 2006b). Sows consumed feed for 9.6 and 21.2 min during heat stress compared with 16.3 and 26.4 min for Large White and Creole sows, respectively. Silva et al. (2009) found similar results in that feeding behavior was affected by season. Nocturnal feed intake was greater than daytime feed intake in multiparous lactating Large White sows. Sow feeding behavior changes from day to night. Typical production practices are to feed lactating sows twice or thrice a day during the daytime hours and do not take advantage of cooler nighttime temperatures for feeding.

Heat stress may exacerbate weight loss during lactation, as this phase of production is typically characterized by weight loss due to mobilization of body reserves for milk production. Sows that were restricted (7.88 Mcal of NE/d) nutritionally during lactation lost 22.4 kg during lactation compared with sows fed 10.51 Mcal of NE/d that

lost 14.0 kg (van den Brand et al., 2000). Regardless of temperature, lesser feed intake alone may extend weaning-to-estrus intervals. Weaning-to-estrus intervals were longer for sows in a thermoneutral environment with restricted feed intake, with no sows returning to estrus within 6 d compared with 83.3% of sows in a thermoneutral environment with *ad libitum* intake with a weaning-to-estrus interval within 6 d (Messias de Braganca et al., 1998). Similar findings were reported when lighter weight sows were less fertile following lactation than heavier sows (Maclean, 1969).

Feeding behavior and intake affect the interval from weaning-to-estrus. In underfed lactating sows, only 63% of sows returned to estrus within 10 d after weaning (van den Brand et al., 2000). Zak et al. (1997) reported weaning-to-estrus intervals were 122.3 h for sows fed a restricted ration during the first 21 d of lactation and 134.7 h for sows restricted fed during the last week of lactation (28 d lactation), while *ad libitum* fed control sows had a weaning-to-estrus interval of 88.7 h. Fat and protein loss increased from 309 and 642 g/d to 483 and 968 g/d for *ad libitum* fed sows exposed to 18 and 29°C, respectively (Quiniou and Noblet, 1999). Apparently, a reduction in feed intake affects body weight loss which impacts the amount of adipose and lean muscle tissue in heat-stressed sows.

Backfat and loin muscle area are two measurements that indicate nutrient mobilization during lactation that may be altered by heat stress. Thermoneutral sows lost 1.5 mm backfat during lactation compared with sows exposed to heat stress that lost 11.7 mm backfat (Barb et al., 1991). During the warm season sows lost 0.12 mm backfat, while sows lost 1.58 mm during the hot season (Dove and Haydon, 1994). Backfat and loin muscle area were reduced when sows were exposed to a constant elevated

temperature during 19 d of lactation (Spencer et al., 2003). Heat-stressed sows lost 1.82 cm² loin muscle area and 3.35 mm backfat, while thermoneutral sows lost 0.46 cm² loin muscle area and 1.15 mm backfat. Johnston et al. (1999) and Quiniou and Noblet (1999), however, did not find differences in backfat for heat-stressed sows and sows in thermoneutral temperatures during lactation. To summarize, feed intake decreases as a result of heat stress, therefore, body weight loss increases and backfat and loin muscle area may be reduced.

Methods to alleviate heat stress

Changing the environment. Producers have attempted to use cooling systems and changes in diet to alleviate the detrimental effects of heat stress. Producers use evaporative cooling strategies in facilities to alleviate heat stress. Evaporative cooling systems work through contact of air with water to remove heat through evaporation (Hellickson and Walker, 1983). Drippers, sprinklers, and evaporative cooling cells are used to lower the ambient temperature in farrowing rooms and gestation/breeding barns (Harmon et al., 2001). Drippers and sprinklers allow for heat evaporation through water contacting the skin. Evaporative cool cells are also used that line the perimeter walls and are effective in keeping rooms cooler than outside temperatures by pulling fresh air through wetted corrugated material. Mechanized ventilation systems (fans) are installed in swine facilities to provide adequate fresh air movement and remove dust, moisture and gases. Often times, operations that use mechanical ventilation combine this method with cool cells to provide maximum comfort to the sows during hot months. The effects of water drips, snout coolers and cool pads on heat stress have been studied.

During heat stress, sows with a water drip had greater feed intake, lost less body weight and weaned heavier piglets when compared with heat-stressed sows without a water drip (McGlone et al., 1988a). Snout coolers attenuated the effects of heat stress for sows ,and feed intake improved but was still lower for sows with snout coolers in 30°C (4.2 kg/d) compared with sows with snout coolers in 18 (6.46 kg/d) and 25°C (6.13 kg/d) (Stansbury et al., 1987). Conductive cool pads reduced respiration rate and rectal temperatures when compared to snout coolers and drip coolers for heat-stressed gilts in pens (Bull et al., 1997). Gilt respiration rates were 72.7, 114.2 and 102.7 bpm, and rectal temperatures were 39.4, 39.8 and 39.7°C for conductive cool pads, snout coolers and drip coolers, respectively. Furthermore, gilts chose cool pads 49.4% of the time over the drip (31.8%) and snout (18.8%) coolers. Changing the environment is one way to effectively relieve heat stress.

Changing the diet. Studies have examined the effects of feed ingredients on alleviating heat stress, as well as how ingredients included in diets have an effect on heat-stressed sows. Diet changes included increasing energy and decreasing crude protein to reduce heat increment, increasing arginine to improve performance during lactation and determining the effects of increased fiber on heat-stressed sows when byproducts were included in the feed. A study was performed to investigate the interaction between energy intake and heat stress and determine if high energy diets could alleviate the negative effects of heat stress on early embryonic mortality. Early gestating sows fed a high energy or normal energy diet during heat stress had decreased intake and nutrient utilization compared with sows in a thermoneutral environment (Liao and Veum, 1994).

The results of this study, therefore, demonstrated no beneficial effects on high energy diets relieving heat stress.

Arginine was added to lactation diets to determine if arginine could improve lactation performance for heat-stressed sows. Heat-stressed (29.4°C, 12 h day; 24°C, 12 h night) sows fed a high level of arginine (1.74%) had a reduced feed intake of 5.01 kg/d compared with heat-stressed sows fed a control diet (1.34% arginine) with an average feed intake of 5.26 kg/d during lactation (Pérez Laspiur and Trottier, 2000). Body weight loss, however, decreased for sows fed a high level of arginine at 4.74 kg compared with control sows that lost 11.24 kg. This indicates that although a high level of arginine did not increase feed intake, sows were more feed efficient when a high level of arginine was added to the lactation diet.

The effect of additional fiber in lactation feed was studied for sows in tropical conditions. High fiber ingredients are available as milling byproducts, and performance of lactating sows was investigated as a result of this dietary change. Inclusion of more fiber was not beneficial to body weight gain in sows. In fact, an increase in dietary fiber caused greater body weight loss in multiparous lactating sows regardless of the season (Renaudeau et al., 2003a). Sows fed a high fiber diet lost 33 kg compared with 17 kg lost by sows fed a control diet.

A reduction in crude protein fed to lactating sows was studied to determine if heat production could be reduced (Silva et al., 2009). In growing pigs, feeding lesser amounts of crude protein in the diet resulted in a reduction in heat production (Le Bellego et al., 2001), and this study hypothesized that sows would also reduce the thermic effect of feed and increase feed intake. Silva et al. (2009) reported that tropical sows fed a reduced

crude protein diet had a depression in intake and meal size during the hot season. Sows consumed 1.2 kg/d less during the hot season, and meal size was decreased by 0.22 kg/meal. This study also determined that sows fed diets with standard amounts of crude protein or a diet supplemented with amino acids were subject to a greater dietary heat increment and were unable to attenuate the effects of heat stress on feed intake.

Effects of heat stress on the piglet and growing pig

Growth performance during lactation

Heat stress during the lactation phase has an effect on piglet survivability and performance. Piglet weaning weight average was 5.84 kg when sows were exposed to 29°C compared with an average of 6.89 kg for piglets from sows in an 18°C environment (Quiniou and Noblet, 1999). Sows heat-stressed at 30°C had litters that weighed 52.39 kg at weaning, which was lighter than sows exposed to 18 and 25°C that had litters that weighed 63.23 and 61.13 kg, respectively (Stansbury et al., 1987). Heat-stressed first and second parity sows (32°C) had litters with depressed average daily gain (Schoenherr et al., 1989). Sows that farrowed in the warm season had pigs that weighed 5.33 kg on d 21 of lactation with an average litter gain of 31.65 kg, while cool season sows had pigs that weighed 5.83 kg with an average litter gain of 36.55 kg (Dove and Haydon, 1994). Creole and Large White sows had piglets that grew better and weighed more at d 21 and at weaning when they farrowed during the warm season compared with the hot season (Gourdine et al., 2006a, b).

Piglet mortality was greater at 0.7 pigs compared with 0.2 for heat-stressed sows (27°C) and thermoneutral sows (18°C), and litter weight gain was depressed during heat stress at 1.58 kg/d compared with 2.15 kg/d (Prunier et al., 1997). In a different study, litter growth rate was 2.1 kg/d during the hot season and 2.3 kg/d during the warm season (Renaudeau et al., 2003a). Another study concluded, however, that preweaning mortality was less during heat stress (30.4°C) when compared with a thermoneutral (23.6°C) temperature (McGlone et al., 1988b). The reason for less preweaning mortality during heat stress could be attributed to the fact that piglets from sows in the thermoneutral environment did not choose to stay under the heat lamp and suffered from cold stress.

Differences in litter weights from heat-stressed sows can be observed as lactation progresses. For example, heat stress reduced litter weight gain with primary differences seen during week 2 of lactation and later with pigs from heat-stressed (30°C) sows gaining 1.6 kg/d and pigs from thermoneutral (20°C) sows gaining 2.0 kg/d over the entire lactation (Messias de Braganca et al., 1998). Likewise, litter weights for multiparous sows were less at three weeks of age because of season with differences in weights varying between 2 and 3 kg depending on parity (Peltoniemi et al., 1999). First parity sows tend to lose more weight during lactation and typically wean lighter piglets than multiparous sows. Furthermore, primiparous sows weaned lighter pigs compared with multiparous sows in a constant high temperature during lactation (Spencer et al., 2003).

As discussed in the previous section, piglet growth was less when sows were heat-stressed because sow milk production was less. A reduction in milk production caused by heat stress resulted in piglets that gained 62 g/d less and weighed 2.0 kg less at weaning

when compared with thermoneutral piglets (Renaudeau and Noblet, 2001). As sow milk production decreased during heat stress, piglets were supplemented with milk replacer to alleviate the effects of heat stress (Azain et al., 1996). Consumption of milk replacer was greater for pigs born during the warm season rather than the cool season and this offset the lesser weaning weights during the warmer months.

Heat stress further aggravates sow body weight loss during lactation to result in lighter pigs. Body weight loss was encouraged during studies by reducing the amount of energy and protein in early gestation and lactation diets in order to examine resulting piglet performance. Reese et al. (1982) characterized the effects of feeding a low energy diet during the first lactation and how this impacted subsequent performance during their second lactation. Sows fed a diet with a low amount of ME during their first lactation gained more weight and had more backfat during the subsequent gestation but farrowed lighter weight piglets at their second farrowing than sows fed a diet high in ME (Reese et al., 1982). Reese et al. (1982) also reported that sows fed a low ME diet during their first lactation weighed 13.4 kg less and had 3.4 mm less backfat after they farrowed their second litter. Furthermore, sows that weighed less with less backfat postpartum had weaning weights 0.6 kg lighter. A decreased amount of protein was fed to sows to simulate protein loss as a result of lactation. Heat stress exacerbates loss of body weight and this study tested the degree of protein loss that could be sustained before milk production was impaired (Clowes et al., 2003). Low maternal protein intake of 491g/d crude protein decreased milk production and caused the greatest change in piglet growth with piglets weighing 11% less between period 1 (d 0 to 20) and period 2 (d 20 to wean).

Performance of weaned pigs

Heat stress causes a thermal response in weaned growing pigs. Christon (1988) reported that growing pigs (8 to 25 kg) exposed to a tropical climate had a rectal temperature of 40.2°C in the afternoon compared with 39.3°C for control pigs, and greater respiration rates in the morning and afternoon of 81.8 and 106.0 bpm, respectively, for heat-stressed and 29.5 bpm and 26.2 bpm, respectively, for control pigs.

Growth and feed intake of weaned pigs is detrimentally affected by heat stress. Weaned pigs from heat-stressed sows are at a disadvantage and may have lesser weight gain and body weight compared with pigs weaned from thermoneutral sows. Piglets exposed to heat stress were less feed efficient compared with control pigs and gained 0.12 kg less per day (Christon, 1988). Similarly, piglets that were heat stressed consumed 280 g DM/d less and gained 163 g/d less than control pigs and had less total heat production that was partially attributed to a lack of physical activity (Collin et al., 2001a). In a second study with contrasting results, acute heat stress for 4 hours in weaned pigs decreased feeding behavior, but body weight gain, feed intake or feed efficiency was not different than control pigs (Hicks et al., 1998). The time period for heat stress may not have been long enough or it was not hot enough to cause a response different from the control pigs. High ambient temperatures reduced feed intake and piglet body weight except when acute heat stress was studied.

Voluntary feed intake and body weight gain were reduced for young pigs with body weights of 20 kg at 35 or 33°C compared with 19 or 23°C according to Collin et al. (2001b,c). Feed intake was constant between 19 and 25°C, but above this temperature there was a decrease of 33 g/d in piglet voluntary feed intake. Furthermore, feed intake

was depressed by 30% and a reduction of 37% in gain was observed for pigs exposed to 33°C compared with pigs in a thermoneutral environment of 23°C (Collin et al., 2001b). Heat-stressed pigs consumed 86 meals/d at 3.1 min/meal compared with thermoneutral pigs that consumed 132 meals/d at 4.6 min/meal after 3 d of exposure to their environments, and this was correlated with the difference in feed intake.

Relatively short exposure to heat stress may affect feed intake and body weight. Ambient temperature was set to 25°C for all pigs 2 d prior to the beginning of 17 d of a constant experimental temperature. On d 2 temperature increased to 27, 29, 31, 33 or 35°C, and each increase in temperature caused an immediate reduction in feed intake and lesser body weight (Collin et al., 2001c). Weaned pigs exposed to acute heat stress were less active, engaged in less aggressive behavior and spent less time feeding than pigs that were not heat-stressed (Hicks et al., 1998). Weaned pigs, therefore, have decreased feed intake, are less feed efficient and have decreased overall growth performance as a result of heat stress.

Performance of growing pigs

Heat stress impacts growth performance of older, growing pigs as well. Growing pigs reared in tropical temperatures had an average rectal temperature of 40.6°C and respiration rate of 101.6 bpm in the afternoon compared with pigs in the control environment with average rectal temperature of 38.4°C and respiration rate of 21.8 bpm (Christon, 1988). Elevated rectal temperatures and respiration rates during heat stress were associated with an increase in skin temperatures. Skin temperature increased in Creole and Large White pigs in response to heat stress in an apparent effort to promote heat dissipation through vasodilation (Renaudeau et al., 2007). Rectal temperatures

increased for both breeds during heat stress. An adaptation to heat stress was noted as rectal temperatures decreased over time, although this response was not evident until 20 d after exposure.

Heat stress affects not only thermal, but also production responses of growing pigs. Grow-finish pigs exposed to two degree increases in ambient temperature demonstrated physiological responses beginning at 22°C (Huynh et al., 2005). Specifically, there was an increase in respiration rate, a decrease in feed intake, a decrease in heat production and an increase in rectal temperature that contributed to poor growth performance. Similar to previous findings, another study reported that finishing pigs in tropical environments had 1.3°C greater rectal temperatures, an increase of 87.7 bpm for respiration rates, 0.36 kg/d less gain, 0.39 kg/d lesser feed intake and were less efficient than pigs in a control environment (Christon, 1988).

Feed intake decreases for growing pigs during heat stress, but growing pigs may possess the ability to adapt to high ambient temperatures. In Creole and Large White growing pigs, average daily feed intake decreased when pigs were exposed to elevated temperatures, but feed intake gradually increased during the remaining days on trial. The increase in feed intake suggested that the pigs were acclimating to the environment (Renaudeau et al., 2007).

Conclusions

The objective of this review was to describe reproduction in sows and how heat stress influences reproduction, thermal and metabolic responses and piglet performance.

Heat stress impacts sows at all phase of production. Repercussions within reproduction include decreased follicular growth, prolonged weaning-to-estrus intervals, early embryonic death and an increase in still born. Sows are less productive and have decreased feed intake and negative energy balance which leads to decreased milk production and, subsequently, decreased piglet performance. Growth performance and thermal response for young, growing pigs are negatively impacted by heat stress. Overall, heat stress affects many aspects of sow reproduction and performance. Further investigations of the mechanisms of heat stress may lead to better management of sows and pigs during heat stress.

CHAPTER 3

RESPONSES OF SOWS TO HEAT STRESS IN A PRODUCTION CYCLE: GENERAL REPRODUCTIVE CHARACTERISTICS

SUMMARY

Heat stress (HS) produces seasonal infertility in sows and decreases reproductive efficiency. The objective of this experiment was to examine productivity in sows exposed to HS during a production cycle (gestation, lactation, and breeding). First parity Landrace or Landrace x Large White F1 sows were rotated through chambers in the Brody Environmental Center for 55 d beginning in late gestation. The ambient temperature sequences included either thermoneutral (TN; 18 to 20°C) or HS (24 to 30°C) for each production phase with the following treatment groups: TN-TN-TN ($n = 15$), TN-HS-TN ($n = 14$), HS-TN-HS ($n = 14$) or HS-HS-HS ($n = 15$) for gestation-farrowing-breeding (20, 24, and 11 d, respectively). General aspects of the thermal and reproductive response were measured. Rectal temperature differed across phases and conditions [38.33 and 38.22, 39.47 and 39.23, 38.79 and 38.74°C (SEM < 0.05)] for HS and TN during gestation, farrowing, breeding, respectively ($P < 0.001$). Body weight gain for sows in gestation was greater for TN sows (14.2 ± 1.1 kg) compared with HS sows (11.7 ± 1.1 kg; $P < 0.022$). Sows in HS-TN-HS lost less body weight during lactation compared with TN-TN-TN, TN-HS-TN and HS-HS-HS sows (-22.2 ± 3.0 , -30.4 ± 3.0 , -32.6 ± 3.0 , and -

30.7 ± 3.0 kg, respectively; $P < 0.084$). There was an effect of treatment on body weight change in breeding sows that came from HS farrowing lost slightly less during breeding (-8.85 ± 1.0 kg) than sows that came from TN farrowing (-10.9 ± 1.0 kg; $P < 0.039$). Sows in TN weaned heavier piglets than HS [6.21 and 5.77 kg (SEM < 0.23), respectively; $P < 0.053$]. Weaning-to-estrus interval (4.70 ± 0.12 d), percentage sows inseminated after weaning (85.7%), subsequent farrowing rate (82.6%) and subsequent total born (10.8 ± 0.3 pigs per litter) were not different by treatment. In summary, HS sows had greater body temperatures during gestation and lactation. Sows in TN-TN-TN and TN-HS-TN gained more weight in gestation compared with HS-HS-HS and HS-TN-HS and sows in TN-TN-TN and HS-TN-HS lost less during lactation compared with HS-HS-HS and TN-HS-TN. Piglet weights at weaning were lighter for HS sows. This may be a consequence of less milk production by HS sows. Heat stress did not have an effect on rebreeding and subsequent farrowing performance.

INTRODUCTION

Seasonal infertility is largely a result of high summertime ambient temperatures and is a phenomenon that is problematic for swine producers because it causes economic loss. Two components of seasonal infertility are anestrus and long weaning-to-estrus intervals (WEI). Messias de Braganca et al. (1998) concluded that sows experience longer WEI in response to elevated ambient temperature conditions during lactation. High ambient temperatures lessen the amount of feed consumed and this impacts reproductive performance through an interaction of nutrition and reproduction (Koketsu

et al., 1996). Indeed, Lucy et al. (2001) observed smaller follicles in heat-stressed sows perhaps because feed intake was less and metabolic hormones affecting follicular growth were reduced. In addition to affecting follicular growth, the reduction in sow feed intake can have adverse effects for growth performance of piglets. For example, high ambient temperature was shown to reduce feed intake in multiparous lactating sows and reduce body weight gain in piglets (Quiniou and Noblet, 1999). Lower body weight gain for piglets has been linked to lesser milk production in sows exposed to high ambient temperatures (Renaudeau and Noblet, 2001). The effect of high ambient temperatures on piglet growth is important because weaning weight is an important performance metric for swine producers (heavier weaned pigs is considered desirable).

Sows move through production facilities in a continuous cycle. Sows are inseminated and remain in the gestation barn until they move to a farrowing room a few days before farrowing. After farrowing, sows remain in the farrowing room and nurse their piglets until weaning. Sows return to the breeding barn to be reinseminated. As sows move through the two buildings (breeding/gestation and farrowing) they experience different environments. Producers may choose to cool their sows within neither, one, or both buildings. The objectives of this research were to determine the thermal, metabolic, litter and reproductive responses of sows exposed to heat stress in a breeding/gestation facility and (or) a farrowing room. With the information gained from this experiment, recommendations will be made to producers regarding facilities that should be cooled to provide the most beneficial response from sows. This new information may be used to change the way sows are managed during periods of expected high seasonal infertility.

MATERIALS AND METHODS

Animals and Facilities

All animal procedures were reviewed and approved by the University of Missouri Animal Care and Use Committee. Primiparous pregnant Landrace or Landrace x Large White sows ($n = 58$) of Monsanto Choice Genetics were brought into the Brody Environmental Center (BEC) between 89 and 93 days of gestation in five groups from December, 2007, through April, 2008. The sows were reared, housed, artificially inseminated (Landrace x Large White or Large White pooled boar semen) and confirmed pregnant at the University Swine Research Complex (Columbia, MO) before being brought to the environmental center. The BEC contains four environmental chambers (each 9.3 x 5.2 m). Two chambers were used for breeding/gestation and two were used for farrowing. The breeding/gestation chambers had 12 gestation stalls (2.4 x 0.6 m) with nipple valve waterers. The front half of the gestation stall floor was solid with the back half comprised of extruded metal to allow for feces and urine to fall into the flush gutter underneath. The farrowing chambers had six farrowing crates (2.1 x 1.5 m; Rohn Agriproducts, Peoria, IL, USA) each that had watering cups and feeders mounted to the front of the crate. Tenderfoot[®] (Tandem Products, Inc., Minneapolis, MN, USA) comprised the flooring of the farrowing crates and can be described as heavy expanded metal covered with a coat of plastisol.

Experimental Design

Upon arrival to the BEC, sows were blocked by body weight and assigned to treatment (randomized block design). Sows moved through the chambers for 55 d

beginning in late gestation, continuing through farrowing/lactation and culminating during the breeding phase. At the start of the trial, sows were housed in a breeding/gestation room where they stayed for 20 d, after which the sows moved into a farrowing room (approximately 111 d of gestation). After parturition, sows nursed their piglets and were weaned on d 44 of the trial (average lactation length = 20.5 ± 1.4 d). Sows moved back into the breeding/gestation room on d 44 where they were housed for the remaining days of the study.

The daily ambient temperature cycles included either thermoneutral (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C). The heat stress cycle was designed to mimic conditions sows experience under commercial conditions in an evaporatively-cooled barn as recorded in the summer of 2007 in Missouri (data not shown). Regardless of treatment, the minimum temperature was held between 0400 and 0800 h and the temperature was then increased in a linear manner to the maximum temperature by 1200 h. The temperature was held at the maximum for 8 hours (i.e., until 2000 h) and then decreased in a linear manner to the minimum temperature by 0400 h. Sows were assigned to one of four treatments that consisted of different environmental temperatures during the different production phases. The treatments are denoted as TN-TN-TN ($n = 15$), TN-HS-TN ($n = 14$), HS-TN-HS ($n = 14$) or HS-HS-HS ($n = 15$), where the series of abbreviations represent the environmental temperature that the sow experienced in gestation-farrowing-breeding (20, 24, and 11 d, respectively). Ambient lighting in the BEC was programmed to turn on at 0615 h (coinciding with the morning feeding) and turn off at 2100 h.

Body Weights and Real-time Ultrasound Measurements

Sows were brought into the BEC and were weighed using a standard heavy duty single animal crate scale with an electronic load cell (Paul Livestock, Duncan, OK, USA). Backfat (BF) depth and loin eye area (LEA) were measured using an Aloka 500V real-time ultrasound machine (Corometrics Medical Systems, Wallingford, CT, USA) fitted with a 3.5 MHz linear array transducer. Backfat depth and LEA measurements were made by using internal calipers within the ultrasound and taken off the dorsal midline at the 10th rib as previously described (Thiel-Cooper et al., 2001). The hair was shaved from the area and the skin was marked with a permanent marker at the vertical boundaries of the shaved area so that the same location could be used for subsequent measurements. Ultrasound measurements were taken and sows were weighed on d 0 (start of trial), d 20 (moved from breeding/gestation room to farrowing room), d 44 (weaning; moved from farrowing to breeding/gestation room) and d 55 (end of trial). Sows were assigned to the HS or TN gestation room at the time initial measurements were recorded (d 0).

Thermal Measurements

Thermal response measurements were taken four times each day at 0800, 1200, 1600 and 2000 h. Rectal temperature was measured with a Model 8110-20 thermistor thermometer (Cole-Parmer Instrument Company, Vernon Hills, IL, USA), respiration rate was calculated by counting breaths per minute (bpm), and skin temperature was taken with an infrared temperature gun (Raytek, Everett, WA, USA). Skin temperature measurements were taken at four different locations (ear, shoulder, rump and base of tail) where the skin was marked with a permanent marker and shaved.

Feeding of Sows

Sows in gestation were fed from rubber feed pans. The sows were fed a corn-soybean meal-based diet once daily at 0615 h (Table 3.1). Feed offered and refused was recorded using an AccuWeigh scale (Model BD11-200PK, Metro Equipment Company, Sunnyvale, CA, USA). Sows were offered 1.8 kg per day. After 45 min, the feed pans were removed and the remaining feed (including any spilled and unconsumed feed) was weighed.

After sows were moved into the farrowing room and had farrowed, they were fed *ad libitum* a corn-soybean meal-based lactation diet (Table 3.1). Feed was offered two times a day at 0615 h and 1400 h. Feed offered was recorded at both feeding times, and remaining feed was removed and the volume was recorded before the afternoon feeding. Sows that had been moved into the farrowing room but had not farrowed were fed 1.8 kg of feed (equally divided into two feedings) before parturition. After parturition, feed offered was increased by 0.9 kg per day increments depending on feed consumption. Sows that consumed the previous meal in its entirety were offered additional feed. Sows that failed to consume the previous meal in its entirety were offered less feed.

Sows were weighed and BF depth and LEA measurements were made when sows were weaned and moved from the farrowing rooms into the breeding rooms where they were fed the same diet used in gestation once daily. The amount of feed offered was based on body condition (thinner sows receiving additional feed and heavier sows receiving less feed). Sows with a body condition score of less than or equal to 2 [based on subjective determination by the feeder; (Patience et al., 1995)] were offered 2.9 to 3.2 kg of feed per day. Sows with an average body condition (3) were offered 2.7 kg per day.

Sows with a body condition of greater than or equal to 4 were fed 1.8 to 2.3 kg per day. Feed was weighed and feed offered and refused were recorded as previously described for gestation.

Reproductive Management before Farrowing

Parturition was induced on d 23 of the trial (approximately d 114 of gestation) by injecting 10 mg of prostaglandin F_{2α} (2 mL Lutalyse®, i.m.; Pfizer Animal Health, New York, NY, USA) followed by injecting 40 units of oxytocin (2 mL i.m.; Vedco, Inc., St. Joseph, MO, USA) 24 h later if the sow did not show signs of impending farrowing (n = 37). If sows (n = 9) showed signs of farrowing the day following injection of prostaglandin F_{2α} then no oxytocin was administered. Sows that farrowed before 114 were not treated with prostaglandin F_{2α} or oxytocin.

Piglet Weights and Management

Two days after farrowing the piglets were weighed using the AccuWeigh scale and routine processing procedures were performed that included ear notching for individual piglet identification, tail docking, castration of male piglets and i.m. injection of 100 mg of supplemental iron (Vedco, Inc.). Piglets were vaccinated with E. coli vaccine (autogenous bacterin; Addison Biological Laboratory, Fayette, MO, USA) and were weighed individually again at d 10 and 21 of age.

Reproductive Management after Weaning

Estrous detection started 3 d after weaning. A mature boar was allowed to walk in front of the gestation stalls twice daily [morning (0900 h) and afternoon (1600 h)] so that sows could be detected in estrus. The back pressure test was applied to each sow while the boar walked in front of the stalls, and sows with an erect and immobile stance were

considered in estrus. Sows in estrus were artificially inseminated with the boar kept in front of the sows during insemination. Sows were inseminated once per day in the morning and were generally inseminated for two or three consecutive days. Estrous detection was performed until all the sows in the group were inseminated or determined to have ovulated based on ultrasound examination. Ultrasound was performed until the last day of the trial for sows that did not express estrus or ovulate. Transrectal ultrasound was performed (as described by Bracken et al., 2003) to monitor follicular development. An Aloka 900 ultrasound machine fitted with a 7.5 MHz linear array transducer was used. Polyvinyl carbonate (PVC) pipe was securely attached to the handle by using Zonas® Tape (Johnson & Johnson Consumer Products Co., New Brunswick, NJ, USA). Starting on the day of weaning, ultrasound was performed on each sow. The ultrasound probe and handle were coated with obstetrical lubricant before being inserted into the rectum. The ovaries were located to the left or right of the midline anterior to the bladder. Ultrasonography continued every other day (i.e., d 0, 2, 4, 6, etc., after weaning) until ovulation or until the end of the trial. Day of ovulation was defined as the day when preovulatory follicles disappeared from the ovary. The Aloka 900 has a built-in video recording feature. Once the ovary was identified, a series of images were captured and used to measure the diameter of five follicles at their maximum size. The five follicles were captured from either ovary depending on the clarity of the image. The mean follicular diameter, median follicular diameter and largest follicle size were determined.

The trial was terminated 11 d after weaning. At that time sows were vaccinated intramuscularly with 5 ml of FarrowSure® (Pfizer Animal Health, Exton, PA, USA) and were transported to a commercial production system. At this farm, sows were

reinseminated if they showed signs of standing estrus (returns or sows not detected before the end of the trial). Sows farrowed and subsequent litter data was collected that included the number born alive, number of still born, preweaning mortality and number of piglets weaned.

Blood Samples for Hormone Assays

Blood samples were collected from sows using jugular venipuncture. A 9 mL Luer Microvette® Z 92 x 16.5 mm tube (Sarstedt, Inc., Newton, NC, USA) and a four inch hypodermic needle (Air-Tite Products Company, Inc., Virginia Beach, VA, USA) were used. Samples were stored temporarily on ice. Samples were obtained on d 15 (gestation room; approximately one week before farrowing), d 29 and 43 (farrowing room; first and third week of lactation), and in the breeding room (d 47; three d after weaning). Blood was centrifuged (15 min at 1500 $\times g$) and serum was collected and frozen at -20°C.

Serum progesterone concentrations were measured for d 15 samples using a Coat-a-Count RIA kit (Diagnostic Procedures Corp., Los Angeles, CA, USA) according to the manufacturer's instructions. Validation of the kit was performed for porcine serum (Liu et al., 2000). Serum estradiol concentrations were measured by radioimmunoassay on d 43 (the day before weaning) and d 47 (three days after weaning) as previously described (Kirby et al., 1997). The estradiol assay was modified because serum sample size for extraction used was 200 μ l. The assay was validated for porcine serum (Liu et al., 2000). The intra-assay coefficient for the estradiol assay was 24.5%.

Statistical Analyses

Data were analyzed using the General Linear Models procedure (PROC GLM) of SAS (SAS Institute Inc., Cary, NC). The experiment was conducted in five groups of

sows that were exposed to one of four treatments (TN-TN-TN, TN-HS-TN, HS-TN-HS, and HS-HS-HS). Data with one observation per sow were analyzed with a model that included the main effects of treatment, group, and treatment by group interaction. The effects of treatment were partitioned into three contrasts denoted as C1 (TN-TN-TN + TN-HS-TN vs. HS-TN-HS + HS-HS-HS; sows in a thermoneutral breeding/gestation room vs. sows in a heat stress breeding/gestation room), C2 (TN-TN-TN + HS-TN-HS vs. TN-HS-TN + HS-HS-HS; sows in a thermoneutral farrowing room vs. sows in a heat stress farrowing room) and C3 (TN-TN-TN + HS-HS-HS vs. TN-HS-TN + HS-TN-HS; treatment interaction). Treatment means were separated by using the Duncan's multiple range test of SAS. Duncan's separates means without any adjustments and is a more liberal test that will give different results than those analyzed by adjusting everything in the model as above. In some cases, data include the effects of day or even time and day (temperature measurements). For these data, a model that included the effects of treatment, group, treatment by group, sow nested within treatment and group (error term for preceding terms), day, time, and all interactions was used. Data means are expressed as least squares means \pm SEM. Data means were considered significant at $P < 0.104$, as this number rounds to 0.10. Proportions were tested by using Chi-square.

RESULTS

General Characteristics of the Thermal Response across the Entire Trial

Rectal temperature. Rectal temperatures were lowest during gestation (first 3 weeks of the trial; $38.38 \pm 0.01^\circ\text{C}$) and increased after farrowing ($39.35 \pm 0.01^\circ\text{C}$; Figure 3.1).

There was a decrease in rectal temperature after weaning ($38.77 \pm 0.01^\circ\text{C}$; d 44). There was an effect of treatment ($P < 0.001$) for rectal temperature because sows housed in HS chambers when they were either gestating (first three weeks of the trial; 38.22 ± 0.02 , 38.22 ± 0.02 , 38.31 ± 0.02 , and $38.35 \pm 0.02^\circ\text{C}$ for TN-TN-TN, TN-HS-TN, HS-TN-HS, and HS-HS-HS, respectively; Table 3.2) or lactating (~ d 23 to 44; 39.22 ± 0.06 , 39.49 ± 0.06 , 39.23 ± 0.06 , and $39.44 \pm 0.06^\circ\text{C}$ for TN-TN-TN, TN-HS-TN, HS-TN-HS, and HS-HS-HS, respectively; Table 3.5) had greater rectal temperatures. After weaning, rectal temperatures were not different among treatments ($P > 0.10$).

Respiration rates. There was an effect of treatment on respiration rates ($P < 0.001$; Figure 3.2). During gestation, respiration rates were greater in sows in the HS chambers (25.75 ± 1.55 , 26.05 ± 1.61 , 43.28 ± 1.61 , and 44.84 ± 1.55 bpm for TN-TN-TN, TN-HS-TN, HS-TN-HS, and HS-HS-HS, respectively; Table 3.2). There was an increase in respiration rate after farrowing, and the increase in respiration rates was greatest for HS sows (33.74 ± 1.84 , 64.43 ± 1.83 , 35.86 ± 1.85 , and 62.90 ± 1.77 bpm for TN-TN-TN, TN-HS-TN, HS-TN-HS, and HS-HS-HS, respectively; Table 3.5). After weaning, respiration rates decreased and remained greater for HS sows (23.31 ± 0.95 , 22.52 ± 0.95 , 31.45 ± 0.92 , and 31.37 ± 0.89 bpm for TN-TN-TN, TN-HS-TN, HS-TN-HS, and HS-HS-HS, respectively; Table 3.7).

Shoulder skin temperature. There was an effect of treatment on shoulder skin temperature ($P < 0.001$; Figure 3.3). During gestation, shoulder skin temperatures were greater for sows in the HS chambers (30.88 ± 0.16 , 30.83 ± 0.17 , 35.20 ± 0.17 , and $35.14 \pm 0.16^\circ\text{C}$ for TN-TN-TN, TN-HS-TN, HS-TN-HS, and HS-HS-HS, respectively; Table 3.2). There was an increase in shoulder skin temperature after farrowing and the increase in shoulder

skin temperature was greatest for HS sows (33.01 ± 0.19 , 37.32 ± 0.18 , 32.94 ± 0.19 , and $37.04 \pm 0.18^\circ\text{C}$ for TN-TN-TN, TN-HS-TN, HS-TN-HS, and HS-HS-HS, respectively; Table 3.5). Shoulder skin temperature progressively increased for TN sows during lactation. After weaning, shoulder skin temperature decreased and remained greater for HS sows (31.17 ± 0.19 , 31.41 ± 0.19 , 35.62 ± 0.18 , and $35.06 \pm 0.18^\circ\text{C}$ for TN-TN-TN, TN-HS-TN, HS-TN-HS, and HS-HS-HS, respectively; Table 3.7).

Sows in Gestation Rooms

Rectal temperature, respiration rate, skin temperature. On the first full day of the trial (gestation room), rectal temperature, respiration rate, and skin temperature differed by treatment ($P < 0.01$; Table 3.2). Contrast 1 was also significant for these measures ($P < 0.001$; sows moved into the HS gestation had greater rectal temperature, respiration rate and skin temperature). On the last full day in the gestation room (d 19), respiration rate and skin temperature remained different between treatments, but rectal temperature did not differ by treatment ($P > 0.10$) but Contrast 1 was $P < 0.045$. The lesser difference in rectal temperature was apparently caused by an increase in rectal temperature from d 1 to 19 in TN sows. Across the entire time period when sows were in gestation, rectal temperature, respiration rate, and skin temperature differed by treatment ($P < 0.001$) and Contrast 1 was significant ($P < 0.001$).

Body weight, backfat depth, and loin eye area. Sows entered the trial (d 0) on day 90.9 ± 0.1 of gestation and were similar for body weight (185.3 ± 1.4 kg) and backfat depth (2.4 ± 0.1 cm; Table 3.3). There were small differences in loin eye area that were unexpected (sows were randomly assigned to treatment within weight block). Sows left gestation 20 d later and were similar for body weight (198.2 ± 1.6 kg). The change in body weight (d

0 to 20), however, was greater for sows in the TN room with sows in the TN room gaining approximately two additional kg when compared with sows in the HS room (Contrast 1; $P < 0.022$). Backfat depth and the change in backfat depth were not affected by treatment. Loin eye area was similar for sows on d 20, but there was an effect of treatment on the change in loin eye area from d 0 to 20 ($P < 0.05$). The HS-HS-HS had a slight gain of loin eye area, but this response was not observed in HS-TN-HS sows that were identically treated to that point of the experiment.

Serum progesterone concentrations. Serum progesterone concentrations were not affected by treatment (Table 3.3).

Animal health. None of the gestating sows required veterinary care (Table 3.3).

Sows in Farrowing Rooms

Farrowing data. The trial day that the sows farrowed (23.5 ± 0.2 d) and the gestation length (114.4 ± 0.2 d) were not affected by treatment (Table 3.4). Contrast 1 was significant ($P < 0.056$) because sows in the HS gestation rooms had the shorter gestation length. Sows were induced to farrow with Lutalyse[®] (15.5%), Lutalyse[®] + oxytocin (63.8%) or were not treated for the purpose of induction (20.7%). There was an effect of treatment because HS-HS-HS sows were induced at a greater frequency in the Lutalyse[®] only group than the other treatments ($P < 0.016$). Contrast 2 was significant with a greater number of HS sows in farrowing induced with Lutalyse[®] only ($P < 0.070$). There was an effect of treatment for the Lutalyse[®] + oxytocin induction ($P < 0.005$). A greater number of sows in TN farrowing were induced with Lutalyse[®] + oxytocin (Contrast 2, $P < 0.014$).

Total born (11.7 ± 0.4 pigs per litter), born alive (11.0 ± 0.3 pigs per litter), still born (0.41 ± 0.10 pigs per litter), mummies (0.29 ± 0.08 pigs per litter), and piglet body weight at processing (1.46 ± 0.06 kg) were not affected by treatment.

Ten sows (17%) required minor assistance at farrowing and five sows (9%) required major assistance at farrowing. There was not an effect of treatment and contrasts were not significant for minor or major assistance at farrowing. Litter size after cross fostering was similar for treatments (10.6 ± 0.2 pigs per litter).

Rectal temperature, respiration rate, skin temperature. Approximately 1 wk after farrowing (d 30 of the trial), rectal temperature, respiration rate, and skin temperature differed by treatment ($P < 0.001$; Table 3.5). Contrast 2 was also significant for these measures ($P < 0.001$; sows moved into the HS farrowing room had greater rectal temperature, respiration rate and skin temperature). On the last full day in the farrowing room (d 43), rectal temperature, respiration rate and skin temperature remained different among treatments ($P < 0.001$) and Contrast 2 was significant at $P < 0.001$. Sows in the HS farrowing room had greater rectal temperature, respiration rate and skin temperature. Across the entire time when sows were in the farrowing room, rectal temperature, respiration rate, and skin temperature differed by treatment ($P < 0.001$) and Contrast 2 was also significant ($P < 0.001$).

Body weight, backfat depth, and loin eye area. Sows entered farrowing on day 110.9 ± 0.1 of gestation and were similar for body weight (198.2 ± 1.6 kg), backfat depth (2.5 ± 0.1 cm), and loin eye area (51.2 ± 0.7 cm 2 ; Table 3.6). Sows left farrowing (d 44) and were similar for body weight (168.6 ± 2.0 kg), backfat depth (2.0 ± 0.1 cm), and loin eye area (47.1 ± 0.7 cm 2). The change in body weight (d 20 to 44), however, was greater for

sows in the HS room compared with sows in the TN room (Contrast 2, $P < 0.079$).

Backfat depth and loin eye area and the change in backfat depth and loin eye area were not affected by treatment.

Litter characteristics at 10 d and at weaning. The number of piglets at weaning (10.3 ± 0.2 pigs per litter) was not affected by treatment (Table 3.4). Piglet body weight at d 10 (3.22 ± 0.07 kg) and piglet weaning weight (5.98 ± 0.11 kg) were not affected by treatment. Contrast 2 was significant for weaning weight ($P < 0.053$) because piglets weaned from sows in a TN farrowing room were heavier. The greater weaning weight was associated with greater sow feed intake for TN sows (Chapter 4).

Animal health. The number of sows that required veterinary care was not affected by treatment (Table 3.4). Two sows in TN-TN-TN, two sows in TN-HS-TN, one sow in HS-TN-HS and one sow in HS-HS-HS were treated for uterine infection (secondary to dystocia) or lameness by using antibiotics or an anti-inflammatory medicine. One TN-TN-TN sow died during lactation because of complications arising from dystocia.

Sows in Breeding Rooms

Rectal temperature, respiration rate, skin temperature. On the first full day in breeding (d 45 of the trial), respiration rate and shoulder skin temperature differed by treatment ($P < 0.01$; Table 3.7). Contrast 1 was also significant for respiration rate and shoulder skin temperature ($P < 0.001$). Rectal temperature was not affected by treatment, perhaps because sows had adapted to the HS temperature. After 1 wk in the breeding room (d 52), respiration rate and skin temperature remained different among treatments ($P < 0.001$) and rectal temperature did not differ by treatment ($P > 0.10$). Contrast 1 was at $P < 0.001$.

Across the entire time sows were in breeding, respiration rate and skin temperature differed by treatment ($P < 0.001$) and Contrast 1 was significant ($P < 0.001$).

Body weight, backfat depth, and loin eye area. Sows entered breeding (d 44) and were similar for body weight (168.6 ± 2.0 kg), backfat depth (2.0 ± 0.1 cm), and loin eye area (47.1 ± 0.7 cm 2 ; Table 3.8). Sows that came from the TN farrowing room had slightly greater loin eye area (Contrast 2; $P < 0.091$). When sows left breeding (d 58), they were similar for body weight (159.7 ± 2.0 kg) and loin eye area (47.7 ± 0.6 cm 2), but there was an effect of treatment on backfat depth (1.9 ± 0.1 cm; $P < 0.095$). Contrast 1 was significant ($P < 0.021$) for backfat depth because backfat depth was slightly greater for HS sows. The change in loin eye area was similar (d 44 to 58), but there was an effect of treatment for body weight and backfat depth change ($P < 0.001$). The change in backfat depth was lesser for HS sows (Contrast 2; $P < 0.001$).

Animal health. Sows that required veterinary care and the number culled during breeding were not affected by treatment (Table 3.8). One TN-TN-TN sow had a rectal tear apparently caused by the transrectal ultrasound exam, and one TN-HS-TN sow had a pinched nerve and was unable to stand on her hind legs. Both of these sows were euthanized during breeding.

Return to estrus after weaning. The proportion of sows that returned to estrus and were inseminated (85.7%) after weaning was not affected by treatment (Table 3.9). Anovulatory sows were comprised of two TN-TN-TN and one TN-HS-TN sow. There was no effect of treatment, but a greater number of sows in TN breeding were anovulatory (Contrast 1, $P < 0.065$). Sows that ovulated as detected by ultrasound but did not express estrus (silent ovulation) included two TN-TN-TN, two HS-TN-HS and one

HS-HS-HS sow. The number of sows with silent ovulations was not affected by treatment. Weaning-to-estrus intervals (4.70 ± 0.12 d) and length of estrus (2.24 ± 0.10 d) were not affected by treatment.

Follicular development after weaning. On the day of weaning (d 0), mean follicle diameter (2.90 ± 0.08 mm) and median follicle diameter (2.86 ± 0.09 mm) were not affected by treatment (Table 3.10). Largest follicle size (3.45 ± 0.09 mm) differed by treatment ($P < 0.047$). Contrast 2 was significant for mean diameter and largest follicle ($P < 0.065$). Sows in the TN farrowing room had slightly larger follicles on d 0. On d 2 after weaning, mean diameter, largest follicle and median diameter were not affected by treatment. Contrast 1 was significant for median diameter ($P < 0.087$) because median follicle diameter was slightly greater for HS-TN-HS sows. On day 4 after weaning, mean diameter, largest follicle and median diameter were not affected by treatment. The small differences in follicle size observed at weaning were not apparent at d 4 after weaning.

Serum estradiol concentrations. Serum estradiol concentrations increased ($P < 0.001$) from 1 d before weaning (1.68 ± 0.12 pg/mL) to 3 d after weaning (14.91 ± 1.30 pg/mL) but were not affected by treatment (Table 3.10).

Characteristics of the second litter. The number of sows that farrowed their second litter (82.6%) was not affected by treatment (Table 3.9). Total born (10.8 ± 0.3 pigs per litter), born alive (10.2 ± 0.3 pigs per litter), and still born (0.61 ± 0.14 pigs per litter) were not affected by treatment.

DISCUSSION

In this experiment, the thermal and reproductive responses of sows to heat stress were studied. Rectal temperature was the lowest during gestation, and HS sows had greater rectal temperatures than TN sows. After farrowing, rectal temperature increased for all treatments (Figure 3.1). This uniform and large increase in body temperature was apparently caused by the increase in energy intake and metabolic rate for the lactating sow. Heat-stressed sows had greater rectal temperatures during lactation when compared with TN sows. After weaning, however, rectal temperature was not different between HS and TN sows. The failure to detect a difference after weaning perhaps suggests that the sows may change their body temperature set point during lactation. This change in set point may be a compensatory mechanism to acclimate to increased heat production during lactation. Data from previous studies are in agreement with our results that show that HS sows have greater rectal temperatures during gestation (Omtvedt et al., 1971; Liao and Veum, 1994) and lactation (Prunier et al., 1997; Messias de Braganca et al., 1998). Surprisingly, heat-stressed sows in a different study, did not have greater rectal temperatures after farrowing and during lactation (Kelley and Curtis, 1978). It is unclear why these investigators failed to observe the large change in rectal temperature that this study determined.

In addition to the aforementioned differences in rectal temperature, greater respiration rates for HS sows were observed (Figure 3.2). This effect was very apparent and existed across the three phases of production. Gestating sows that were HS had greater respiration rates that increased further after farrowing. The further increase in respiration rates for HS during lactation may indicate that the lactating sows are

experiencing a greater metabolic load (with associated heat production) and are attempting to cool their bodies through a respiratory mechanism. When the sows were weaned, respiration rates decreased, but HS sows retained a greater respiration rate when compared with TN. An interesting observation was that the HS and TN sows in breeding had lesser respiration rates when compared with HS and TN sows in gestation (Figure 3.2). These lesser respiration rates in breeding sows were found despite an apparently greater rectal temperature (relative to gestation) for sows in the breeding phase (Figure 3.1). As implied in the preceding paragraph, it appeared that sows adapt to the metabolic heat of lactation by changing their thermoregulatory set point. The change in set point led to a reduced respiration rate response in weaned HS sows within the breeding room. Greater respiration rates in gestation and lactation for HS sows were also observed in other studies (Machado-Neto et al., 1987; Liao and Veum, 1994; Spencer et al., 2003).

Regardless of the production phase (gestation, farrowing, or breeding) shoulder skin temperatures were greater for sows that were exposed to HS (Figure 3.3). This response was somewhat predictable in that skin temperature is partly determined by the environmental temperature and the peripheral vasodilation that occurs in response to environmental temperature. After farrowing, skin temperatures increased for sows in both HS and TN rooms. The HS sows had the greatest skin temperature, and the increase in shoulder skin temperature was rapid and sustained. The pattern of change for shoulder skin temperature was distinctly different for TN sows. In TN sows, shoulder temperature increased progressively during lactation reaching a maximum by the last third of lactation. The increase in shoulder skin temperature was associated with changes in feed intake (Chapter 4), perhaps suggesting that the TN sows were increasing in terms of

metabolic activity. The HS sows were fully vasodilated early in lactation with shoulder skin temperatures that approached body temperature. This scenario (skin temperature approaching body temperature) is indicative of full vasodilation of blood vessels. The HS sows, therefore, were incapable or further vasodilation. After weaning, skin temperatures followed the same pattern as respiration rates in that skin temperatures decreased for all sows while HS remained greater. The skin temperature was nearly equivalent to what was observed in gestating sows. This equivalent skin temperature was observed despite greater body temperature in sows after weaning. This again indicates that the weaned sows had a changed body temperature set point and that mechanisms such as vasodilation are not invoked in an effort to reduce body temperature to a level equivalent to that found in late gestation. Our observations for skin temperature are similar to that observed by other researchers (Quiniou and Noblet, 1999; Renaudeau et al., 2003b).

Sows that were heat-stressed during late gestation had greater rectal temperature, respiration rate and skin temperature with lesser differences observed for rectal temperature on the last day of gestation. This may be attributed to a slight increase in rectal temperatures for TN sows as parturition approached. Under thermoneutral conditions, therefore, an increase in heat production from the pregnancy was detected that apparently caused a slight increase in body temperature. For some reason, the TN sows did not attempt to alleviate this increase in body temperature by appreciably increasing respiration rate or skin temperature.

The HS sows gained less body weight than TN during gestation. Sows were fed the same and consumed equivalent amounts of feed in gestation (Chapter 4). The lesser body weight for HS, therefore, cannot be attributed to depressed feed intake caused by

HS. Energy balance (Chapter 4) was also not affected by treatment. The apparent differences in body weight were perhaps caused by additional energy demands for thermoregulation (not accounted for in energy balance calculations). It is also possible that HS sows had become slightly dehydrated. A change in backfat depth was not detected for sows by the end of gestation, so the composition of the weight loss was not backfat. Loin eye area was greater for HS-HS-HS sows, but this effect was not observed in the HS-TN-HS group that was in the same environment.

Heat stress during gestation had a minimal effect on farrowing. Gestation length was not affected by treatment. A difference in gestation length would be difficult to detect given our experimental system that employed timed induction of parturition with Lutalyse® and oxytocin. It was interesting to note that sows moving from a HS gestation to HS farrowing (HS-HS-HS sows) were less likely to be treated with both Lutalyse® and oxytocin (Table 3.4). This indicates that perhaps these sows were starting to farrow earlier than the other groups. There were no treatment effects on total born, born alive, still born, mummies or piglet body weight at processing. Sows were HS during late gestation (as opposed to early gestation) and this may be one reason for the lack of differences in litter data.

Body weight loss in farrowing was less for HS-TN-HS sows (Table 3.6). These same sows had the heavier piglets at weaning than TN-HS-TN or HS-HS-HS sows. Heat stress in the farrowing room appeared to lead to lower-weight weaned pigs (Table 3.4). Others have demonstrated that piglets raised by HS sows have decreased body weights at weaning (Quiniou and Noblet, 1999). The observation that the HS-TN-HS sows lost less weight and weaned heavier pigs is certainly of interest. One conclusion is that the HS-

TN-HS sows were in more positive energy balance during lactation and that this more positive energy balance led to lesser weight loss and greater milk production. This possibility will be explored in Chapter 4.

After weaning, sows in the HS breeding/gestation room had greater respiration rates and skin temperatures, and these measures remained greater through the end of the trial. There were no differences in rectal temperature during breeding. This lack of difference in rectal temperature indicates that in both groups body temperature set point had increased and there was no apparent effort by TN sows to reduce body temperature further. There were no treatment differences for body weight, backfat depth or loin eye area when the sows entered breeding; however, TN sows had slightly greater loin eye area. On the last day of the trial, there was no effect of treatment on body weight and loin eye area. There was a small difference in backfat with HS sows having slightly greater backfat depth. Sows in TN may have lost more backfat because they were too cool. During the entire breeding period, HS sows lost less backfat and HS-HS-HS sows lost less body weight. The fact that HS sows lost less backfat and body weight in breeding was clearly unexpected; particularly because their feed intake during this period was less as well (Chapter 4). All treatment groups lost body weight in breeding. This was unexpected as well because the calculated energy balance of the sows was positive during this time (Chapter 4). One possibility for less body weight and backfat depth loss for HS sows is that the HS environment enabled a lower maintenance energy requirement so that the weight loss for HS sows was less than TN sows.

Gross measures of reproductive performance were not affected by treatment. There were no differences in weaning-to-estrus intervals, the number of anestrus sows, or

the number of sows with silent ovulations (Table 3.9). Overall, the sows on this trial had very acceptable reproductive performance regardless of treatment group. Previous studies have reported prolonged weaning-to-estrus intervals (Cox et al., 1983; Clark et al., 1986) and an increase in the incidence of anestrus (Teague et al., 1968; Johnston et al., 1999) for HS sows. No affects were observed on the subsequent litter. This again was unexpected because one consequence of seasonal infertility is low farrowing rates and low litter size. A critical question that arises from this work is why didn't the HS sows have a loss in reproductive performance? A number of possibilities exist. One obvious question was whether or not an adequate stress was applied to the sows. The maximum temperature applied was 30°C for approximately 8 h. The humidity in the chambers was not controlled and, therefore, was equivalent to outside air humidity in mid-Missouri from December through May (averaging about 65%). It is very likely that sows in commercial barns would experience greater humidity in the summer and a greater heat index in the summer. It is also possible that the regular temperature cycle that the sows experienced enabled an acclimation to high ambient temperatures that could not be achieved under natural weather conditions that can create erratic ambient temperatures inside swine barns. In addition to the possibility that inadequate stress was applied, was a second possibility that sows with certain genetic lines are less susceptible to heat stress. The sows used in this study were Monsanto Choice Genetics, and this line of sows may be better able to overcome the deleterious effects of summer heat stress.

Follicular growth was measured using ultrasound. This was done to determine if the treatments applied had an impact on the development of ovarian follicles. Follicles were measured at the time of weaning and then on alternate days thereafter. There was an

effect of treatment on follicular growth because on the day of weaning the average diameter of the largest follicle and the mean follicular diameter were greatest for sows in the HS-TN-HS treatment. This same treatment group lost the least weight in farrowing and weaned heavier pigs. Their weight profile and piglet weaned weight implies a more positive energy balance during lactation (Chapter 4) that apparently impacted their follicular growth as well. By d 2 after weaning greater follicular development in the HS-TN-HS group was clearly gone owing to the rapid period of follicular growth after weaning that eliminated the small advantage held by the HS-TN-HS treatment. In these sows, therefore, a small increase in follicular size, that was perhaps conferred by a more positive energy balance, was not sustained when stronger drivers of follicular growth (primarily the increase in LH pulsatility after weaning) were invoked after weaning. Although differences in follicular growth were not observed, another study indicated a delay in follicular growth for HS sows (Lucy et al., 2001). The sows in the aforementioned study were of entirely different genetics and were also exposed to a more severe heat stress. These factors may explain the differences in the two studies.

In summary, heat stress caused an increase in rectal temperatures, respiration rates and skin temperatures. Sows in farrowing responded to heat stress by large increases in these thermal measurements. After weaning, the decrease in metabolic load led to a decreased thermal response, although rectal temperature did not decrease to reach temperatures observed during gestation. Heat-stressed sows gained less weight during gestation than TN, regardless that there was no difference in feed intake. The reason for the differences in weight gain may be attributed to the possibility that HS sows had to expend more energy cooling their bodies. Sow body weight loss during lactation was less

in HS-TN-HS resulting in heavier piglets at weaning than HS sows. These sows were better able to partition nutrients toward milk production as well as body maintenance. Sows continued to lose weight during breeding, while HS sows lost less body weight and backfat. One reason for this may be because these sows lost more weight during lactation and had less to lose during breeding. Repercussions were not observed for weaning-to-estrus intervals, the incidence of anestrus or subsequent farrowing performance. Differences in follicular growth were noted on the day of weaning, and HS-TN-HS sows had larger follicles. The larger follicle size may be one advantage of increased feed intake (Chapter 4) and a more positive energy balance at the end of lactation. This difference was short lived, and follicle size did not differ by d 2 after weaning. The lack of detrimental effects on reproduction may be attributed to differences between the environmental center and commercial production systems. Many production factors could contribute to these differences, including management and other environmental conditions. The heat stress that was applied may not have been adequate, and the sows may have adapted to the cycle within the chambers. It can be concluded that sows are most sensitive to heat stress during lactation. Sows that were heat-stressed had an increased thermal response that resulted in decreased piglet growth and greater sow body weight loss at weaning. Producers choosing to alleviate heat stress should focus their cooling efforts during this phase of production. Future investigations on heat stress are needed to further characterize reproductive responses for sows in a commercial production system.

Table 3.1. Composition of lactation and gestation/breeding diets (% as-fed basis).

Item	Lactation diet	Gestation/Breeding diet
Corn	64.6	69.4
Soybean meal (48%)	28.3	15.0
Soy hulls	-	10.0
Choice white grease	2.5	1.0
Dicalcium phosphate	2.4	2.3
Limestone	0.8	1.0
Salt	0.5	0.5
Lysine	0.1	-
Vitamin premixes	0.5	0.5
Trace mineral premix	0.2	0.2
Zinc and biotin premixes	0.2	0.2

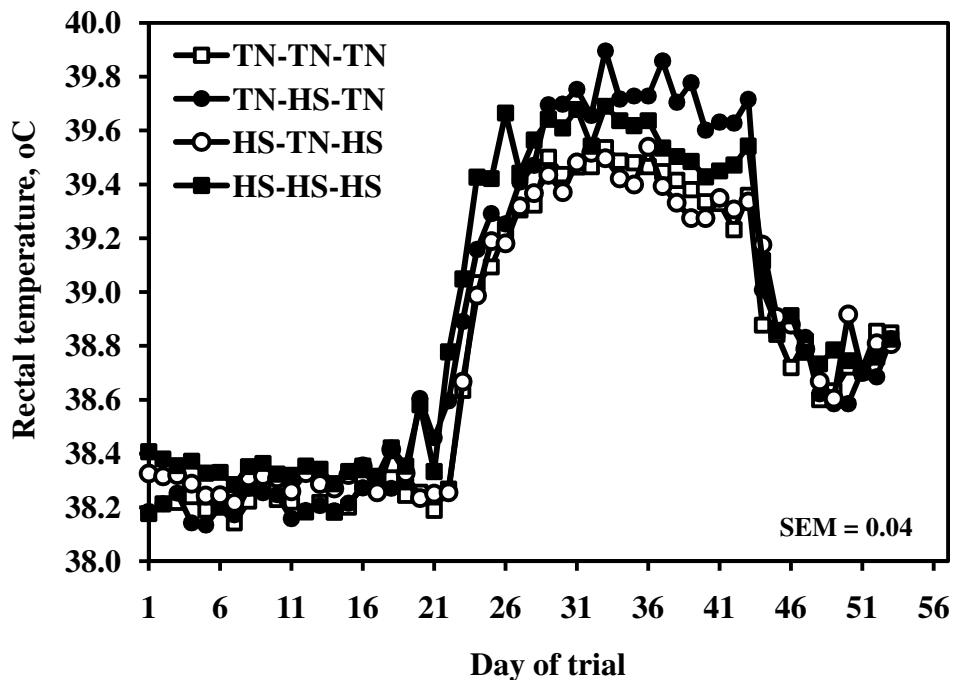


Figure 3.1. Least squares means for rectal temperature of sows exposed to different ambient temperature treatments across 55 d of the trial. Treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding. Sows were in gestation from d 0 to 20, farrowing from d 20 to 44, and breeding after d 44.

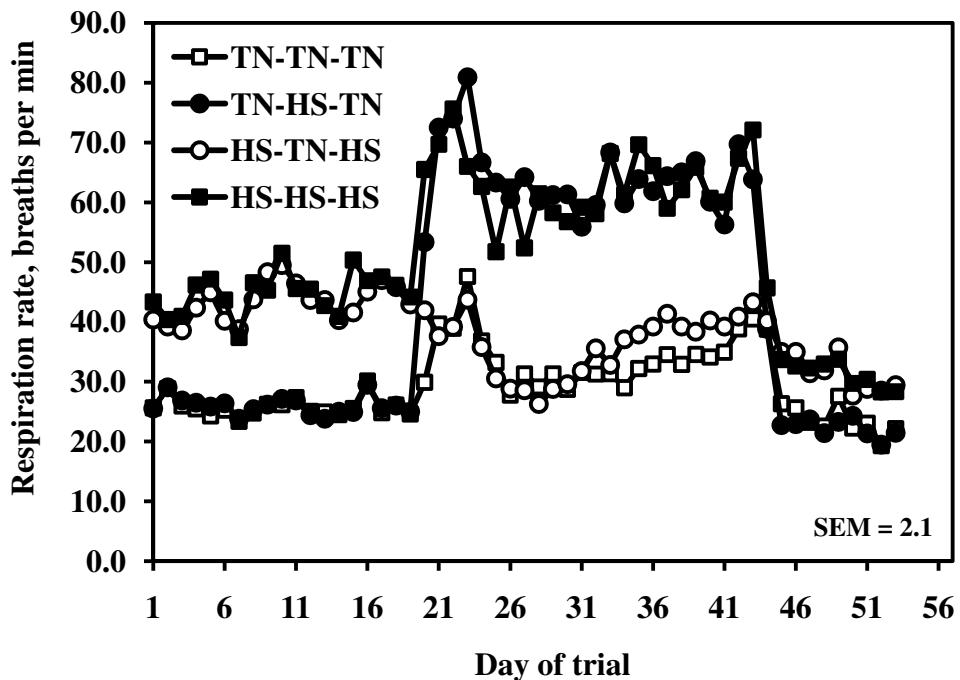


Figure 3.2. Least squares means for respiration rate of sows exposed to different ambient temperature treatments across 55 d of the trial. Treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding. Sows were in gestation from d 0 to 20, farrowing from d 20 to 44, and breeding after d 44.

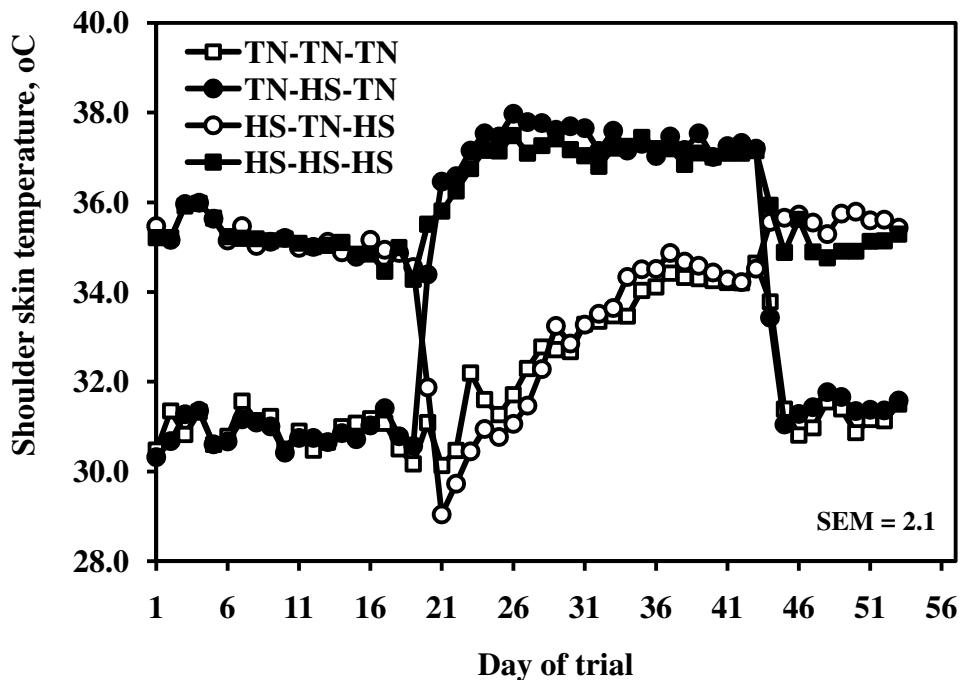


Figure 3.3. Least squares means for skin shoulder temperature of sows exposed to different ambient temperature treatments across 55 d of the trial. Treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding. Sows were in gestation from d 0 to 20, farrowing from d 20 to 44, and breeding after d 44.

Table 3.2. Rectal temperature, respiration rate, and shoulder skin temperature for pregnant sows on the first full day in the gestation room (d 1), the last full day in the gestation room (d 19), and across the entire gestation.

	N	Treatment ¹						P< ²
		TN-TN-TN	TN-HS-TN	HS-TN-HS	HS-HS-HS	Trt	C1	
First full day in gestation (Day 1)								
Rectal temperature, °C	38.18 ± 0.05	38.19 ± 0.05	38.33 ± 0.05	38.41 ± 0.05	0.005	0.001	NS	NS
Respiration rate, bpm	25.70 ± 2.35	25.59 ± 2.40	40.39 ± 2.40	43.33 ± 2.32	0.001	0.001	NS	NS
Shoulder skin temp, °C	30.46 ± 0.30	30.30 ± 0.30	35.48 ± 0.30	35.21 ± 0.29	0.001	0.001	NS	NS
Last full day in gestation (Day 19)								
Rectal temperature, °C	38.25 ± 0.03	38.30 ± 0.04	38.34 ± 0.04	38.35 ± 0.03	NS	0.045	NS	NS
Respiration rate, bpm	24.63 ± 2.42	25.07 ± 2.50	43.07 ± 2.53	43.96 ± 2.45	0.001	0.001	NS	NS
Shoulder skin temp, °C	30.17 ± 0.28	30.55 ± 0.29	34.59 ± 0.29	34.29 ± 0.28	0.001	0.001	NS	NS
Entire gestation								
Rectal temperature, °C	38.22 ± 0.02	38.31 ± 0.02	38.35 ± 0.02	0.001	0.001	NS	NS	NS
Respiration rate, bpm	25.75 ± 1.55	26.05 ± 1.61	43.28 ± 1.61	44.84 ± 1.55	0.001	0.001	NS	NS
Shoulder skin temp, °C	30.88 ± 0.16	30.83 ± 0.17	35.20 ± 0.17	35.14 ± 0.16	0.001	0.001	NS	NS

¹The treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding.

²Overall type I error rate (P value) for treatment (Trt) and individual treatment contrasts denoted as C1 (TN-TN-TN + TN-HS-TN vs. HS-TN-HS + HS-HS-HS; sows in a thermoneutral breeding/gestation room vs. sows in a heat stress breeding/gestation room), C2 (TN-TN-TN + HS-TN-HS vs. TN-HS-TN + HS-HS-HS; sows in a thermoneutral farrowing room vs. sows in a heat stress farrowing room) and C3 (TN-TN-TN + HS-HS-HS vs. TN-HS-TN + HS-TN-HS; treatment interaction).

Table 3.3. Body weight, back fat depth, and loin eye area for pregnant sows on the first full day in the gestation room (d 1), the last full day in the gestation room (d 19), the change in body weight, back fat depth, and loin eye area during gestation, serum progesterone (d 15), and the number of sows that required veterinary care.

	Treatment ¹			P< ²		
	TN-TN-TN N 15	TN-HS-TN 14	HS-TN-HS 15	Trt	C1	C2
Sows entering gestation (d 1)						
Day of gestation	91.2 ± 0.3	90.9 ± 0.3	90.4 ± 0.3	91.1 ± 0.3	NS	NS
Body weight, kg	184.1 ± 2.7	185.7 ± 2.8	187.3 ± 2.8	183.7 ± 2.7	NS	NS
Backfat depth, cm	2.4 ± 0.1	2.4 ± 0.1	2.6 ± 0.1	2.4 ± 0.1	NS	NS
Loin eye area, cm ²	52.5 ± 1.0 ^{a,b}	51.5 ± 1.1 ^{a,b}	53.7 ± 1.1 ^a	50.0 ± 1.0 ^b	0.102	0.033
Sows leaving gestation (d 19)						
Day of gestation	111.2 ± 0.3	110.9 ± 0.3	110.4 ± 0.3	111.1 ± 0.3	NS	NS
Body weight, kg	198.7 ± 3.2	199.5 ± 3.4	198.6 ± 3.4	195.8 ± 3.4	NS	NS
Backfat depth, cm	2.4 ± 0.1	2.5 ± 0.1	2.7 ± 0.1	2.5 ± 0.1	NS	NS
Loin eye area, cm ²	51.8 ± 1.3	49.9 ± 1.4	51.4 ± 1.4	51.8 ± 1.3	NS	NS
Change (entering to leaving)						
Body weight, kg	14.6 ± 1.0 ^a	13.8 ± 1.1 ^{a,b}	11.4 ± 1.1 ^b	12.0 ± 1.1 ^{a,b}	NS	0.022
Backfat depth, cm	0.03 ± 0.06	-0.01 ± 0.07	0.04 ± 0.07	0.02 ± 0.06	NS	NS
Loin eye area, cm ²	-2.03 ± 1.12 ^b	-2.57 ± 1.19 ^b	-2.68 ± 1.19 ^b	1.43 ± 1.12 ^a	0.050	NS
Serum progesterone (d 15), ng/mL	25.45 ± 2.26	23.02 ± 2.26	23.27 ± 2.26	26.03 ± 2.26	NS	NS
Number required veterinary care	0	0	0	0	NS	NS

¹The treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding.

²Overall type I error rate (P value) for treatment (Trt) and individual treatment contrasts denoted as C1 (TN-TN-TN + TN-HS-TN vs. HS-TN-HS + HS-HS-HS; sows in a thermoneutral breeding/gestation room vs. sows in a heat stress breeding/gestation room), C2 (TN-TN-TN + HS-TN-HS vs. TN-HS-TN + HS-HS-HS; sows in a thermoneutral farrowing room vs. sows in a heat stress farrowing room) and C3 (TN-TN-TN + HS-HS-HS vs. TN-HS-TN + HS-TN-HS; treatment interaction). ^{a,b}Treatment means having different superscript letters differ ($P < 0.05$; Duncan's multiple range test).

Table 3.4. Day of farrowing, gestation length, number of sows per induction protocol, litter information at birth, number of sows that required assistance at farrowing, litter information after fostering, piglet weights at birth, 10 d and weaning, number of sows that required veterinary care and number of sows that died during lactation.

	Treatment					$P <^2$		
	TN-TN-TN	TN-HS-TN	HS-TN-HS	HS-HS-HS	Trt	C1	C2	C3
N	15	14	14	15	-	-	-	-
Trial day at farrowing	23.5 ± 0.4	24.0 ± 0.4	23.7 ± 0.4	23.0 ± 0.4	NS	NS	NS	0.097
Gestation length, d	114.7 ± 0.3	114.9 ± 0.3	114.2 ± 0.3	114.1 ± 0.3	NS	0.056	NS	NS
Induction protocol								
Lutalyse® only, n	2	1	0	6	0.016	NS	0.070	0.015
Lutalyse® + oxytocin, n	11	10	12	4	0.005	NS	0.014	0.024
Litters at birth								
Total born, n	11.5 ± 0.7	11.7 ± 0.7	11.6 ± 0.7	11.8 ± 0.7	NS	NS	NS	NS
Born alive, n	10.9 ± 0.6	10.8 ± 0.7	11.3 ± 0.7	11.0 ± 0.6	NS	NS	NS	NS
Still born, n	0.40 ± 0.20	0.47 ± 0.21	0.13 ± 0.21	0.60 ± 0.20	NS	NS	NS	NS
Mummies, n	0.27 ± 0.16	0.50 ± 0.16	0.20 ± 0.16	0.20 ± 0.16	NS	NS	NS	NS
BW at processing, kg	1.47 ± 0.13	1.40 ± 0.11	1.40 ± 0.11	1.57 ± 0.11	NS	NS	NS	NS
Minor assistance at farrowing, ³ n	3	3	1	3	NS	NS	NS	NS
Major assistance at farrowing, n ⁴	0	1	3	1	NS	NS	NS	NS
Litters after cross fostering								
Litter size, n	10.5 ± 0.4	10.8 ± 0.4	10.5 ± 0.4	10.5 ± 0.4	NS	NS	NS	NS
Number weaned, n	10.3 ± 0.4	10.6 ± 0.4	10.3 ± 0.4	10.2 ± 0.3	NS	NS	NS	NS
BW at 10 d, kg	3.45 ± 0.14	3.13 ± 0.14	3.22 ± 0.12	3.13 ± 0.12	NS	NS	NS	NS
BW at weaning, kg	6.37 ± 0.25	5.73 ± 0.24	6.05 ± 0.21	5.80 ± 0.21	NS	NS	0.053	NS
Number required veterinary care	2	2	1	1	NS	NS	NS	NS
Number died during lactation	1	0	0	0	NS	NS	NS	NS

¹The treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding.

²Overall type I error rate (P value) for treatment (Trt) and individual treatment contrasts denoted as C1 (TN-TN-TN + TN-HS-TN vs. HS-TN-HS + HS-HS-HS; sows in a thermoneutral breeding/gestation room vs. sows in a heat stress breeding/gestation room), C2 (TN-TN + HS-TN-HS vs. TN-HS-TN + HS-HS-HS; sows in a thermoneutral farrowing room vs. sows in a heat stress farrowing room) and C3 (TN-TN-TN + TN-HS-HS vs. TN-HS-TN + HS-TN-HS; treatment interaction). ³Two or fewer piglets were pulled. ⁴More than two piglets were pulled.

Table 3.5. Rectal temperature, respiration rate, and shoulder skin temperature for lactating sows one week after farrowing (d 30), the last full day in the farrowing room (d 43), and across the entire lactation.

	Treatment ¹			P < ²			
	TN-TN-TN	TN-HS-TN	HS-TN-HS	Tr	C1	C2	C3
N	15	14	14	15	-	-	-
Day 30 (-1 wk after farrowing)							
Rectal temperature, °C	39.42 ± 0.09	39.70 ± 0.09	39.38 ± 0.09	39.61 ± 0.08	0.036	NS	0.005
Respiration rate, bpm	28.43 ± 3.00	61.38 ± 3.00	29.57 ± 3.00	56.78 ± 2.90	0.001	NS	0.001
Shoulder skin temp, °C	32.65 ± 0.33	37.68 ± 0.33	32.87 ± 0.33	37.17 ± 0.32	0.001	NS	0.001
Last full day in farrowing (Day 43)							
Rectal temperature, °C	39.36 ± 0.11	39.72 ± 0.10	39.37 ± 0.11	39.54 ± 0.09	0.052	NS	0.013
Respiration rate, bpm	40.48 ± 4.41	63.88 ± 3.91	43.09 ± 4.41	72.10 ± 3.78	0.001	NS	0.001
Shoulder skin temp, °C	34.66 ± 0.22	37.17 ± 0.20	34.75 ± 0.22	37.15 ± 0.19	0.001	NS	0.001
Entire farrowing							
Rectal temperature, °C	39.22 ± 0.06	39.49 ± 0.06	39.23 ± 0.06	39.44 ± 0.06	0.003	NS	0.001
Respiration rate, bpm	33.74 ± 1.85	64.43 ± 1.83	35.86 ± 1.85	62.90 ± 1.77	0.001	NS	0.001
Shoulder skin temp, °C	33.01 ± 0.19	37.32 ± 0.18	32.94 ± 0.19	37.04 ± 0.18	0.001	NS	0.001

¹ The treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding.

²Overall type I error rate (P value) for treatment (Tr) and individual treatment contrasts denoted as C1 (TN-TN-TN + TN-HS-TN vs. HS-TN-HS + HS-HS-HS; sows in a thermoneutral breeding/gestation room vs. sows in a heat stress breeding/gestation room), C2 (TN-TN-TN + HS-TN-HS vs. TN-HS-TN + HS-HS-HS vs. TN-HS-TN + HS-TN-HS; treatment sows in a heat stress farrowing room) and C3 (TN-TN-TN + HS-TN-HS; treatment interaction).

Table 3.6. Body weight, backfat depth, and loin eye area for pregnant sows on the first full day in the farrowing room (d 20), for lactating sows on the last day in the farrowing room (d 44), and the change in body weight, backfat depth, and loin eye area during lactation.

	Treatment ¹						P < ²		
	TN-TN-TN	TN-HS-TN	HS-TN-HS	HS-HS-HS	Trt	C1	C2	C3	
N	15	14	14	15	-	-	-	-	-
Sows entering farrowing (Day 20)									
Day of gestation	111.2 ± 0.3	110.9 ± 0.3	110.4 ± 0.3	111.1 ± 0.3	NS	NS	NS	NS	0.102
Body weight, kg	198.7 ± 3.2	199.5 ± 3.4	198.6 ± 3.4	195.8 ± 3.4	NS	NS	NS	NS	NS
Backfat depth, cm	2.4 ± 0.1	2.5 ± 0.1	2.7 ± 0.1	2.5 ± 0.1	NS	NS	NS	NS	NS
Loin eye area, cm ²	51.8 ± 1.3	49.9 ± 1.4	51.4 ± 1.4	51.8 ± 1.3	NS	NS	NS	NS	NS
Sows leaving farrowing (Day 44)									
Body weight, kg	167.0 ± 4.0	166.9 ± 4.0	176.5 ± 4.0	164.9 ± 3.8	NS	NS	NS	NS	NS
Backfat depth, cm	2.0 ± 0.1	1.9 ± 0.1	2.1 ± 0.1	2.0 ± 0.1	NS	NS	NS	NS	NS
Loin eye area, cm ²	48.2 ± 1.4	45.2 ± 1.4	48.8 ± 1.4	47.0 ± 1.3	NS	0.091	NS	NS	NS
Change (entering to leaving)									
Body weight, kg	-30.4 ± 3.0 ^b	-32.6 ± 3.0 ^b	-22.2 ± 3.0 ^a	-30.7 ± 3.0 ^b	0.084	0.101	0.079	NS	NS
Backfat depth, cm	-0.48 ± 0.09	-0.52 ± 0.09	-0.50 ± 0.09	-0.48 ± 0.08	NS	NS	NS	NS	NS
Loin eye area, cm ²	-3.00 ± 1.42	-4.39 ± 1.42	-2.08 ± 1.42	-4.38 ± 1.34	NS	NS	NS	NS	NS

¹The treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding.

²Overall type I error rate (P value) for treatment (Trt) and individual treatment contrasts denoted as C1 (TN-TN-TN + TN-HS-TN vs. HS-TN-HS + HS-HS-HS; sows in a thermoneutral breeding/gestation room vs. sows in a heat stress breeding/gestation room), C2 (TN-TN-TN + HS-TN-HS vs. TN-HS-TN + HS-HS-HS; sows in a thermoneutral farrowing room vs. sows in a heat stress farrowing room) and C3 (TN-TN-TN + HS-HS-HS vs. TN-HS-TN + HS-TN-HS; treatment interaction).

^{a,b}Treatment means having different superscript letters differ ($P < 0.05$; Duncan's multiple range test).

Table 3.7. Rectal temperature, respiration rate, and shoulder skin temperature for sows on the first full day in the breeding room (d 45), after one week in the breeding room (d 52), and across the entire breeding period.¹

	N	Treatment ¹			P< ²			
		TN-TN-TN	TN-HS-TN	HS-TN-HS	HS-HS-HS	Trt	C1	C2
First full day in breeding (Day 45)								
Rectal temperature, °C	38.83 ± 0.07	38.88 ± 0.07	38.91 ± 0.07	38.86 ± 0.07	NS	NS	NS	NS
Respiration rate, bpm	26.06 ± 1.25	22.98 ± 1.25	35.05 ± 1.22	33.80 ± 1.19	0.001	0.001	0.085	NS
Shoulder skin temp, °C	31.36 ± 0.32	31.03 ± 0.32	35.69 ± 0.31	34.94 ± 0.30	0.001	0.001	0.086	NS
One week in breeding (Day 52)								
Rectal temperature, °C	38.84 ± 0.08	38.69 ± 0.08	38.82 ± 0.07	38.76 ± 0.07	NS	NS	NS	NS
Respiration rate, bpm	19.06 ± 1.30	19.69 ± 1.30	28.50 ± 1.25	28.32 ± 1.21	0.001	0.001	NS	NS
Shoulder skin temp, °C	31.10 ± 0.27	31.34 ± 0.27	25.63 ± 0.26	35.14 ± 0.25	0.001	0.001	NS	NS
Entire breeding								
Rectal temperature, °C	38.74 ± 0.06	38.74 ± 0.06	38.79 ± 0.06	38.79 ± 0.06	NS	NS	NS	NS
Respiration rate, bpm	23.31 ± 0.95	22.52 ± 0.95	31.45 ± 0.92	31.37 ± 0.89	0.001	0.001	NS	NS
Shoulder skin temp, °C	31.17 ± 0.19	31.41 ± 0.19	35.62 ± 0.18	35.06 ± 0.18	0.001	0.001	NS	0.038

¹The treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding.

²Overall type I error rate (P value) for treatment (Trt) and individual treatment contrasts denoted as C1 (TN-TN-TN + TN-HS-TN vs. HS-TN-HS + HS-HS-HS; sows in a thermoneutral breeding/gestation room vs. sows in a heat stress breeding/gestation room), C2 (TN-TN-TN + HS-TN-HS vs. TN-HS-TN + HS-HS-HS; sows in a thermoneutral farrowing room vs. sows in a heat stress farrowing room) and C3 (TN-TN-TN + HS-HS-HS vs. TN-HS-TN + HS-TN-HS; treatment interaction).

Table 3.8. Body weight, backfat depth, and loin eye area for sows on the first day in the breeding room (d 44), the last full day in the breeding room (d 55), the change in body weight, backfat depth, and loin eye area during breeding, the number of sows that required veterinary care and the number of sows culled during breeding.

	Treatment ¹					P < ²		
	TN-TN-TN	TN-HS-TN	HS-TN-HS	HS-HS-HS	Trt	C1	C2	C3
Number entering breeding	14	14	14	15	-	-	-	-
Sows entering breeding (Day 44)								
Body weight, kg	167.0 ± 4.0	166.9 ± 4.0	176.5 ± 4.0	164.9 ± 3.8	NS	NS	NS	NS
Backfat depth, cm	2.0 ± 0.1	1.9 ± 0.1	2.1 ± 0.1	2.0 ± 0.1	NS	NS	NS	NS
Loin eye area, cm ²	48.2 ± 1.4	45.2 ± 1.4	48.8 ± 1.4	47.0 ± 1.3	NS	NS	0.091	NS
Sows leaving breeding (Day 55)								
Body weight, kg	155.9 ± 4.2	159.0 ± 4.2	166.0 ± 4.0	157.2 ± 3.8	NS	NS	NS	NS
Backfat depth, cm	1.7 ± 0.1 ^a	1.7 ± 0.1 ^b	2.1 ± 0.1 ^a	1.9 ± 0.1 ^{a,b}	0.095	0.021	NS	NS
Loin eye area, cm ²	47.4 ± 1.2	47.1 ± 1.2	49.1 ± 1.1	46.9 ± 1.1	NS	NS	NS	NS
Change (entering to leaving)								
Body weight, kg	-11.3 ± 1.0 ^b	-10.0 ± 1.0 ^{a,b}	-10.5 ± 0.9 ^{a,b}	-7.7 ± 0.9 ^a	0.059	NS	0.039	NS
Backfat depth, cm	-0.24 ± 0.05 ^b	-0.27 ± 0.05 ^b	-0.05 ± 0.04 ^a	-0.07 ± 0.04 ^a	0.001	0.001	NS	NS
Loin eye area, cm ²	-0.49 ± 0.92	1.05 ± 0.92	0.33 ± 0.88	-0.17 ± 0.84	NS	NS	NS	NS
Number required veterinary care in breeding	1	1	0	0	NS	NS	NS	NS
Number culled during breeding	1	1	0	0	NS	NS	NS	NS

¹The treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding.

²Overall type I error rate (P value) for treatment (Trt) and individual treatment contrasts denoted as C1 (TN-TN-TN + TN-HS-TN vs. HS-TN-HS + HS-HS-HS; sows in a thermoneutral breeding/gestation room vs. sows in a heat stress breeding/gestation room), C2 (TN-TN-TN + HS-TN-HS vs. TN-HS-TN + HS-HS-HS; sows in a thermoneutral farrowing room vs. sows in a heat stress farrowing room) and C3 (TN-TN-TN + HS-HS-HS vs. TN-HS-TN + HS-TN-HS; treatment interaction).

^{a,b}Treatment means having different superscript letters differ ($P < 0.05$; Duncan's multiple range test).

Table 3.9. Number of sows inseminated, number of sows that were anovulatory or had silent ovulation (ovulation without observed estrus), weaning-to-estrus intervals, length of estrus during breeding and second litter information.

	Treatment ¹					<i>P</i> < ²		
	TN-TN-TN	TN-HS-TN	HS-TN-HS	HS-HS-HS	Trt	C1	C2	C3
N ³	14	13	14	15	-	-	-	-
Estrus and inseminated, n (%)	10 (71)	12 (92)	12 (86)	14 (93)	NS	NS	NS	NS
Anovulatory, n (%)	2 (14)	1 (8)	0 (0)	0 (0)	NS	0.065	NS	NS
Silent ovulation, n (%)	2 (14)	0 (0)	2 (14)	1 (7)	NS	NS	NS	NS
Weaning-to-estrus interval, d	4.7 ± 0.3	4.8 ± 0.3	4.8 ± 0.3	4.7 ± 0.2	NS	NS	NS	NS
Length of estrus, d	2.3 ± 0.2	2.2 ± 0.2	2.1 ± 0.2	2.3 ± 0.2	NS	NS	NS	NS
Second farrowing								
N ⁴	9	12	11	14				
Number farrowing (%)	8 (89)	10 (83)	9 (82)	11 (79)	NS	NS	NS	NS
Total born, n	10.4 ± 0.7	11.5 ± 0.6	10.7 ± 0.7	10.6 ± 0.6	NS	NS	NS	NS
Born alive, n	9.8 ± 0.6	10.5 ± 0.5	10.3 ± 0.5	10.2 ± 0.5	NS	NS	NS	NS
Still born, n	0.63 ± 0.30	1.00 ± 0.27	0.33 ± 0.28	0.45 ± 0.26	NS	NS	NS	NS

¹The treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding.

²Overall type I error rate (*P* value) for treatment (Trt) and individual treatment contrasts denoted as C1 (TN-TN-TN + TN-HS-TN vs. HS-TN-HS + HS-HS-HS; sows in a thermoneutral breeding/gestation room vs. sows in a heat stress breeding/gestation room), C2 (TN-TN-TN + HS-TN-HS vs. TN-HS-TN + HS-HS-HS; sows in a thermoneutral farrowing room vs. sows in a heat stress farrowing room) and C3 (TN-TN-TN + HS-HS-HS vs. TN-HS-TN + HS-TN-HS; treatment interaction).

³Excludes 1 TN-TN-TN sow that died in farrowing and 1 TN-HS-TN sow that was lame (euthanized at breeding).

⁴Excludes 1 HS-TN-HS sow that died on the producer's farm and 1 TN-TN-TN sows that had a rectal tear (euthanized at breeding).

Table 3.10. Mean, largest and median follicle sizes at d 0, 2 and 4 after weaning and serum estradiol concentrations 1 day before and 3 days after weaning.

	N	Treatment ¹						<i>P</i> < ²
		TN-TN-TN	TN-HS-TN	HS-TN-HS	HS-HS-HS	Trt	C1	C2
Day 0 follicles								
Mean diameter, mm	2.93 ± 0.16 ^{ab}	2.92 ± 0.16 ^{ab}	3.16 ± 0.16 ^a	2.61 ± 0.16 ^b	NS	NS	0.084	0.100
Largest follicle, mm	3.39 ± 0.17 ^{ab}	3.45 ± 0.18 ^{ab}	3.85 ± 0.18 ^a	3.14 ± 0.17 ^b	0.047	NS	0.065	0.032
Median diameter, mm	2.84 ± 0.17	2.90 ± 0.18	3.12 ± 0.18	2.59 ± 0.17	NS	NS	NS	0.093
Day 2 follicles								
Mean diameter, mm	3.73 ± 0.20	3.58 ± 0.20	3.90 ± 0.18	3.95 ± 0.18	NS	NS	NS	NS
Largest follicle, mm	4.47 ± 0.22	4.21 ± 0.22	4.50 ± 0.20	4.42 ± 0.19	NS	NS	NS	NS
Median diameter, mm	3.65 ± 0.20	3.54 ± 0.20	3.87 ± 0.18	3.98 ± 0.18	NS	0.087	NS	NS
Day 4 follicles								
Mean diameter, mm	5.46 ± 0.29	4.84 ± 0.30	5.36 ± 0.31	5.55 ± 0.28	NS	NS	NS	NS
Largest follicle, mm	6.41 ± 0.32	5.50 ± 0.33	6.27 ± 0.35	6.21 ± 0.31	NS	NS	NS	NS
Median diameter, mm	5.52 ± 0.29	4.99 ± 0.30	5.33 ± 0.31	5.60 ± 0.28	NS	NS	NS	NS
Serum estradiol, pg/ml								
1 d before weaning	1.27 ± 0.24	1.96 ± 0.24	1.98 ± 0.24	1.53 ± 0.23	NS	NS	NS	0.020
3 d after weaning	13.73 ± 2.61	12.71 ± 2.61	18.25 ± 2.73	15.22 ± 2.49	NS	NS	NS	NS

¹The treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding.

²Overall type I error rate (*P* value) for treatment (Trt) and individual treatment contrasts denoted as C1 (TN-TN-TN + TN-HS-TN vs. HS-TN-HS + HS-HS-HS; sows in a thermoneutral breeding/gestation room vs. sows in a heat stress breeding/gestation room), C2 (TN-TN-TN + HS-TN-HS vs. TN-HS-TN + HS-HS-HS; sows in a thermoneutral farrowing room vs. sows in a heat stress farrowing room) and C3 (TN-TN-TN + HS-HS-HS vs. TN-HS-TN + HS-TN-HS; treatment interaction).

^{a,b}Treatment means having different superscript letters differ (*P* < 0.05; Duncan's multiple range test).

CHAPTER 4

RESPONSES OF SOWS TO HEAT STRESS IN A PRODUCTION CYCLE: METABOLIC CHARACTERISTICS

SUMMARY

The sow responds to heat stress (HS) by reducing feed intake, which promotes a negative energy balance and a decrease in blood IGF-I available for follicular growth. This metabolic mechanism reduces reproductive efficiency for HS sows. The objective of this study was to examine the metabolic response of sows exposed to HS during a production cycle (gestation, lactation, and breeding). First parity Landrace or Landrace x Large White F1 sows were rotated through chambers in the Brody Environmental Center for 55 d beginning in late gestation. The ambient temperature sequences included either thermoneutral (TN; 18 to 20°C) or HS (24 to 30°C) for each production phase with the following treatment groups: TN-TN-TN ($n = 15$), TN-HS-TN ($n = 14$), HS-TN-HS ($n = 14$) or HS-HS-HS ($n = 15$) for gestation-farrowing-breeding (20, 24, and 11 d, respectively). Blood samples were taken to measure concentrations of IGF-I, glucose and NEFA on d 15 (gestation), d 29 (after sows had farrowed), d 43 (one day before weaning) and d 47 (breeding). Feed intake was recorded daily (gestation, breeding) or twice daily (farrowing) and feed refusal was recorded daily for all phases. The response to heat stress was measured. Feed intake differed across treatments (2.8 ± 0.1 , 2.6 ± 0.1 , 2.9 ± 0.1 , and

2.5 ± 0.1 kg/d for TN-TN-TN, TN-HS-TN, HS-TN-HS and HS-HS-HS, respectively) throughout the trial ($P < 0.035$). Energy balance also differed across treatments (-0.3 ± 0.3 , -0.6 ± 0.3 , 0.2 ± 0.3 , and -0.8 ± 0.3 Mcal ME/d for TN-TN-TN, TN-HS-TN, HS-TN-HS and HS-HS-HS, respectively; $P < 0.074$). There was an effect of day on IGF-I concentrations (46.59 ± 2.98 , 85.59 ± 3.04 , 97.91 ± 2.56 , and 104.06 ± 2.60 ng/mL for d 15, 29, 43 and 47, respectively; $P < 0.001$), and HS-TN-HS sows had the greatest concentration of IGF-I on the day before weaning (d 43; 116.11 ± 8.92 mg/mL). In summary, HS sows consumed less feed during lactation. Sows with decreased feed intake had a more negative energy balance as a result of HS. Sows in HS-TN-HS had the greatest feed intake and had a more positive energy balance by the end of lactation. These sows had greater serum IGF-I concentrations the day before weaning. In conclusion, HS had a negative effect on feed intake, energy balance and IGF-I concentrations. Switching a sow from a HS environment during late gestation to a TN environment during farrowing caused an increase in feed intake. The increase in feed intake and the more-positive energy balance may increase milk production (benefitting the piglet), increase IGF-I, and stimulate follicular growth.

INTRODUCTION

Feed intake is one of the primary drivers of metabolic heat production. To reduce metabolic heat production, heat-stressed sows reduce feed intake. One of the primary production responses of sows to heat stress, therefore, is a reduction in feed intake (Teague et al., 1968; Prunier et al., 1997; Renaudeau et al., 2001). The reduction in feed

consumption during HS is especially evident during lactation because sows are fed *ad libitum*.

The lactating sow initially has a negative energy balance after farrowing but generally obtains a more neutral or positive energy balance during the second half of lactation. Sows that are heat-stressed continue to stay in a negative energy balance for the duration of lactation and for a few days after weaning. Heat-stressed sows fail to consume enough feed to achieve a positive energy balance. Low energy results in decreased milk production and an increase in lipid mobilization (Noblet and Etienne, 1986).

After parturition, IGF-I increases but then slowly declines as lactation progresses (Lucy, 2008). Sows with decreased feed intake as a result of heat stress, however, experience a decrease in blood IGF-I. Metabolites are important in regulating follicular growth, and a decrease in IGF-I caused a reduction in follicle size by the end of lactation (Hunter et al., 2004). A delay in return to estrus and an increase in the incidence of anestrous sows may occur because of a decrease in IGF-I concentrations.

If heat stress reduces feed intake and causes negative energy balance then it may also affect hormones and metabolites that respond to the nutrient balance of the sow. The objectives of this research were to measure feed intake, energy balance and metabolite concentrations in sows that were either thermoneutral or heat-stressed. Sows were either maintained in a continuously HS environment (HS-HS-HS), a continuously TN environment (TN-TN-TN) or switched between environments (HS-TN-HS or TN-HS-TN) during gestation, lactation, and breeding, respectively. In this manner the effects of

HS were assessed during different phases of the production cycle and it was determined if changing environments affected the overall response.

MATERIALS AND METHODS

Animals and Facilities

All animal procedures were reviewed and approved by the University of Missouri Animal Care and Use Committee. Primiparous pregnant Landrace or Landrace x Large White sows ($n = 58$) of Monsanto Choice Genetics were brought into the Brody Environmental Center (BEC) between 89 and 93 d of gestation in five groups from December, 2007, through April, 2008. The sows were reared, housed, artificially inseminated (Landrace x Large White or Large White pooled boar semen) and confirmed pregnant at the University Swine Research Complex (Columbia, MO) before being brought to the environmental center. The BEC contains four environmental chambers (each 9.3 x 5.2 m). Two chambers were used for breeding/gestation and two were used for farrowing. The breeding/gestation chambers had 12 gestation stalls (2.4 x 0.6 m) with nipple valve waterers. The front half of the gestation stall floor was solid with the back half comprised of extruded metal to allow for feces and urine to fall into the flush gutter underneath. The farrowing chambers had six farrowing crates (2.1 x 1.5 m; Rohn Agriproducts, Peoria, IL, USA) each that had watering cups and feeders mounted to the front of the crate. Tenderfoot[®] (Tandem Products, Inc., Minneapolis, MN, USA) comprised the flooring of the farrowing crates and can be described as heavy expanded metal covered with a coat of plastisol.

Experimental Design

Upon arrival to the BEC, sows were blocked by body weight and assigned to treatment (randomized block design). Sows moved through the chambers for 55 d beginning in late gestation, continuing through farrowing/lactation and culminating during the breeding phase. At the start of the trial, sows were housed in a breeding/gestation room where they stayed for 20 d, after which the sows moved into a farrowing room (approximately 111 d of gestation). After parturition, sows nursed their piglets and were weaned on d 44 of the trial (average lactation length = 20.5 ± 1.4 d). Sows moved back into the breeding/gestation room on d 44 where they were housed for the remaining days of the study.

The daily ambient temperature cycles included either thermoneutral (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C). The heat stress cycle was designed to mimic conditions sows experience under commercial conditions in an evaporatively-cooled barn as recorded in the summer of 2007 in Missouri (data not shown). Regardless of treatment, the minimum temperature was held between 0400 and 0800 h and the temperature was then increased in a linear manner to the maximum temperature by 1200 h. The temperature was held at the maximum for 8 h (i.e., until 2000 h) and then decreased in a linear manner to the minimum temperature by 0400 h. Sows were assigned to one of four treatments that consisted of different environmental temperatures during the different production phases. The treatments are denoted as TN-TN-TN ($n = 15$), TN-HS-TN ($n = 14$), HS-TN-HS ($n = 14$) or HS-HS-HS ($n = 15$), where the series of abbreviations represent the environmental temperature that the sow experienced in gestation-farrowing-breeding (20, 24, and 11 d, respectively). Ambient lighting in the

BEC was programmed to turn on at 0615 h (coinciding with the morning feeding) and turn off at 2100 h.

Body Weights

Sows were brought into the BEC and were weighed using a standard heavy duty single animal crate scale with an electronic load cell (Paul Livestock, Duncan, OK, USA). Sows were weighed on d 0 (start of trial), d 20 (moved from breeding/gestation room to farrowing room), d 44 (weaning; moved from farrowing to breeding/gestation room) and d 55 (end of trial). Sows were assigned to the HS or TN gestation room after the body weight was recorded (d 0).

Feeding of Sows

Sows in gestation were fed from rubber feed pans. The sows were fed a corn-soybean meal-based diet once daily at 0615 h (Chapter 3;Table 3.1). Feed offered and refused was recorded using an AccuWeigh scale (Model BD11-200PK, Metro Equipment Company, Sunnyvale, CA, USA). Sows were offered 1.8 kg per day. After 45 minutes, the feed pans were removed and the remaining feed (including any spilled and unconsumed feed) was weighed.

After sows were moved into the farrowing room and they had farrowed, they were fed *ad libitum* a corn-soybean meal-based lactation diet (Chapter 3; Table 3.1). Feed was offered two times a day at 0615 and 1400 h. Feed offered was recorded at both feeding times, and remaining feed was removed and the volume was recorded before the afternoon feeding. Sows that had been moved into the farrowing room but had not farrowed were fed 1.8 kg of feed (equally divided into two feedings) before parturition. After parturition, feed offered was increased by 0.9 kg per day increments depending on

feed consumption. Sows that consumed the previous meal in its entirety were offered additional feed. Sows that failed to consume the previous meal in its entirety were offered less feed.

Sows were weaned and moved from the farrowing rooms into the breeding rooms where they were fed the same diet they were fed during gestation once daily. The amount of feed offered was based on body condition (thinner sows receiving additional feed and heavier sows receiving less feed). Sows with a body condition score of less than or equal to 2 [based on subjective determination by the feeder; (Patience et al., 1995)] were offered 2.9 to 3.2 kg of feed per day. Sows with an average body condition (3) were offered 2.7 kg per day. Sows with a body condition of greater than or equal to 4 were fed 1.8 to 2.3 kg per day. Feed was weighed and feed offered and refused were recorded as previously described for gestation.

Blood Samples for Hormone Assays

Blood samples were collected from sows using jugular venipuncture. A 9 mL Luer Microvette® Z 92 x 16.5 mm tube (Sarstedt, Inc., Newton, NC, USA) and a four inch hypodermic needle (Air-Tite Products Company, Inc., Virginia Beach, VA, USA) were used. Samples were stored temporarily on ice. Samples were obtained on d 15 (gestation room; approximately 1 wk before farrowing), d 29 and 43 (farrowing room; first and third week of lactation), and in the breeding room (d 47; 3 d after weaning). Blood was centrifuged (15 min at 1,500 $\times g$) and serum was collected and frozen at -20°C.

Glucose concentrations were determined for d 15, 29, 43 and 47 using a liquid glucose reagent set according to the manufacturer's instructions (Pointe Scientific, Inc., Canton, MI, USA). The glucose assay was run using a 96 well microplate. The standard

was pipetted into one row of wells in 10 µL. The standard curve amounts included 0, 10, 50, and 100 mg/dL, and a high and low serum control were included. Sow serum samples were added to the remaining wells in 10 µl aliquots in duplicate. The reagent was added using 200 µl to each well. The microplate was incubated in a water bath at 37°C for 10 min. After incubation, the microplate was taken to the plate reader (Spectra Rainbow Thermo, Tecan Group Ltd., Männedorf, Switzerland) and glucose concentrations in the samples were analyzed at a wavelength of 500 nm.

Nonesterified fatty acid concentrations were measured for d 15, 29, 43 and 47 using the Wako NEFA-HR(2) Microtiter Procedure (Wako Diagnostics, Richmond, VA, USA) with modifications. Color Reagent Solutions A and B were prepared according to package instructions. A 96 well microplate was used and 2 µl of the serum samples, 5 µl of the calibrator and saline was added. Next, 200 µl of Color Reagent A Solution was added to the microplate. The samples were mixed and incubated at 37°C for 5 min. Color Reagent B Solution was added in 100 µl amounts. The samples were mixed again and incubated at 37°C for another 5 min. The absorbance of each well was measured at 550 nm. The absorbance was plotted against the concentration to construct the calibration curve. The concentrations in the standard curve included 0, 62.5, 125, 250, 500 and 1,000 mg/dL. The microplate reader was used to measure NEFA concentrations in the samples.

Insulin-like growth factor I concentrations were measured for d 15, 29, 43 and 47 using radioimmunoassay (Liu et al., 2000). All samples were run in the same assay. The intraassay coefficient of variation was 7%.

Energy Balance

Energy balance (Mcal) was estimated using energy requirements for each production phase and was based on the following equations (Noblet et al., 1990; NRC, 1998). Regardless of phase, metabolizable energy of intake (ME_I) was calculated by using the energy in the feed multiplied by the feed consumed by the sow. For sows in gestation, maintenance requirements (ME_M) were estimated by using the equation 105 Kcal metabolizable energy per kg of body weight^{0.75} (Noblet et al., 1990). The body weight used was the body weight for sows at the start of the trial. For uterine and mammary growth in gestation, metabolizable energy (ME_{U+M}) was calculated by using the equation ((total piglets born*(3.075*day of gestation + 102.33)*0.239)/1000) – (((8.5*day of gestation + 446.33)*0.239)/1000). The total energy required in gestation was calculated as $ME_M + ME_{U+M}$.

Sows were not weighed after they farrowed. The body weight after farrowing, therefore, was estimated by taking the body weight of the sow when she entered farrowing and subtracting 1.68 kg for each piglet born. The body weight during each day of lactation was then estimated by performing a linear iteration between the starting estimated body weight and the body weight when sows left the farrowing room. In lactation, maintenance requirements were estimated by using the equation 110 Kcal metabolizable energy per kg of body weight^{0.75} (Noblet et al., 1990). Metabolizable energy for milk production (ME_{Milk}) was calculated: (((2540*piglet average daily gain)*(78.7*piglet body weight) +153)*number of piglets in litter)/1000)). The total energy required in lactation was calculated as $ME_M + ME_{Milk}$.

For sows in breeding, maintenance requirements (ME_M) were estimated using the equation 105 Kcal metabolizable energy per kg of body weight^{0.75} (Noblet et al., 1990). The body weight used was the body weight for sows at the start of breeding. The total energy required in breeding was calculated as ME_M .

Sow energy balance for gestation (EB_G), lactation (EB_L) and breeding (EB_B) were determined according to the following formulas (NRC, 1998) and expressed as Mcal of ME/d.

$$EB_G = ME_I - ME_M - ME_{U+M}$$

$$EB_L = ME_I - ME_M - ME_{Milk}$$

$$EB_B = ME_I - ME_M$$

Statistical Analyses

Data were analyzed using the General Linear Models procedure (PROC GLM) of SAS (SAS Institute Inc., Cary, NC). The experiment was conducted in five groups of sows that were exposed to one of four treatments (TN-TN-TN, TN-HS-TN, HS-TN-HS, and HS-HS-HS). Data with one observation per sow were analyzed with a model that included the main effects of treatment, group, and treatment by group interaction. The effects of treatment were partitioned into three contrasts denoted as C1 (TN-TN-TN + TN-HS-TN vs. HS-TN-HS + HS-HS-HS; sows in a thermoneutral breeding/gestation room vs. sows in a heat stress breeding/gestation room), C2 (TN-TN-TN + HS-TN-HS vs. TN-HS-TN + HS-HS-HS; sows in a thermoneutral farrowing room vs. sows in a heat stress farrowing room) and C3 (TN-TN-TN + HS-HS-HS vs. TN-HS-TN + HS-TN-HS; treatment interaction). Treatment means were separated by using the Duncan's multiple range test of SAS. . Duncan's separates means without any adjustments and is a more

liberal test that will give different results than those analyzed by adjusting everything in the model as above. In some cases, data include the effects of day. For these data, a model that included the effects of treatment, group, treatment by group, sow nested within treatment and group (error term for preceding terms), day, and all interactions was used. Data means are expressed as least squares means \pm SEM and considered significant at $P < 0.104$, as this rounds to 0.10.

RESULTS

Metabolic Characteristics of the Sows

Feed Intake. Sows were limit fed during gestation (2.3 ± 0.1 kg; Figure 4.1A). After farrowing sows were fed *ad libitum*, and feed intake increased (3.4 ± 0.1 kg). Sows were limit fed after weaning and feed intake was lowest (1.7 ± 0.1 kg). There was an effect of treatment ($P < 0.001$) for feed intake because HS lactating sows had lesser feed intake (3.6 ± 0.2 , 3.1 ± 0.2 , 4.0 ± 0.2 , and 3.1 ± 0.2 kg for TN-TN-TN, TN-HS-TN, HS-TN-HS, and HS-HS-HS, respectively; Table 4.1). There was an effect of treatment on cumulative feed intake in lactation, and sows in HS-TN-HS consumed more feed than TN-HS-TN and HS-HS-HS sows (90.6 ± 4.0 , 71.8 ± 4.0 and 71.0 ± 3.8 kg, respectively; $P < 0.003$; Table 4.2). There was no difference in feed intake between HS-TN-HS and TN-TN-TN sows in lactation. Cumulative feed intake during gestation and breeding were not affected by treatment.

Feed intake was analyzed according to lactation day. There was an effect of treatment during lactation. Sows that came from HS gestation to TN farrowing had the

greatest daily lactation feed intake (4.1 ± 0.2 kg; Figure 4.2A). Sows that stayed in TN from gestation to farrowing had greater feed intake (3.7 ± 0.2) than HS-HS-HS (3.1 ± 0.2 kg) or TN-HS-TN (3.3 ± 0.2 kg) sows. After weaning, there was no effect of treatment, but sows that came from HS lactation and went into HS breeding consumed the least feed (1.9 ± 0.1 kg). Sows that came from TN lactation had greater feed intake (1.7 ± 0.1 and 1.7 ± 0.1 kg for TN-TN-TN and HS-TN-HS, respectively) in breeding when compared with sows that came from HS lactation (1.9 ± 0.1 and 1.5 ± 0.1 kg for TN-HS-TN and HS-HS-HS, respectively).

Energy balance. Energy balance was greatest during gestation (1.8 ± 0.1 Mcal ME/d) and decreased during lactation (-2.8 ± 0.1 Mcal ME/d; Figure 4.1B). After weaning there was an increase in energy balance (0.7 ± 0.1 Mcal ME/d). Energy balance was not different by treatment during gestation, however, HS-TN-HS (1.7 ± 0.2 Mcal ME/d; Table 4.1) sows had slightly lower energy balance than TN-TN-TN (1.8 ± 0.2 Mcal ME/d), TN-HS-TN (1.8 ± 0.2 Mcal ME/d)and HS-HS-HS (1.8 ± 0.2 Mcal ME/d) sows. There was an effect of treatment on energy balance in farrowing. Energy balance was less negative for HS-TN-HS sows than TN-TN-TN, TN-HS-TN and HS-HS-HS sows during lactation (-1.4 ± 0.5 , -2.9 ± 0.5 , -3.6 ± 0.5 , and -3.6 ± 0.5 Mcal ME/d; $P < 0.005$). Sows in HS-TN-HS reached a positive energy balance by the end of lactation (Figure 4.2B). There was no effect of treatment during breeding, but TN-HS-TN sows had slightly greater energy balance than TN-TN-TN, HS-TN-HS and HS-HS-HS sows (1.3 ± 0.4 , 0.8 ± 0.4 , 0.6 ± 0.4 , and 0.3 ± 0.3 Mcal ME/d; respectively).

Cumulative energy balance was not affected by treatment during gestation (Table 4.2). Sows in HS-TN-HS had less negative cumulative energy balance than TN-HS-TN

and HS-HS-HS sows during lactation (-30.5 ± 10.4 , -80.1 ± 10.4 , and -80.8 ± 9.9 Mcal ME, respectively; $P < 0.004$). Sows in TN had less negative cumulative energy balance than HS sows (Contrast 2, $P < 0.003$). There was no effect of treatment on cumulative energy balance in breeding.

Metabolizable energy in intake (ME_I). Metabolizable energy intake was not affected by treatment during gestation (Table 4.1). During lactation, sows in HS-TN-HS (13.3 ± 0.6 Mcal ME/d) had greater ME_I than TN-TN-TN, TN-HS-TN or HS-HS-HS sows (12.0 ± 0.6 , 10.6 ± 0.6 and 10.5 ± 0.5 Mcal ME/d, respectively; $P < 0.001$). Sows in TN-HS-TN had slightly greater ME_I (6.2 ± 0.4 Mcal ME/d) than the other treatment groups during breeding (5.6 ± 0.4 , 5.7 ± 0.4 , and 5.1 ± 0.4 Mcal ME/d for TN-TN-TN, HS-TN-HS, and HS-HS-HS). Cumulative ME_I was not affected by treatment for gestation and breeding. Sows in HS-TN-HS had greater cumulative ME_I than TN-HS-TN and HS-HS-HS sows during lactation (305.1 ± 13.4 , 241.7 ± 13.4 , and 239.1 ± 12.8 Mcal ME, respectively; $P < 0.003$). Sows in TN farrowing had greater cumulative ME_I than HS sows (Contrast 2, $P < 0.001$).

Metabolizable energy for maintenance (ME_M). There was no effect of treatment for ME_M for sows during gestation, farrowing or breeding (Table 4.1). The ME_M was slightly greater for HS-TN-HS sows, followed by TN-HS-TN, TN-TN-TN and HS-HS-HS for all phases of production. There was no effect of cumulative ME_M for sows in gestation, farrowing or breeding (Table 4.2).

Requirements above maintenance. Energy requirements above maintenance were not different by treatment during gestation or farrowing (Table 4.1). During farrowing, sows in TN had slightly greater requirements above maintenance than HS sows. Cumulative

requirements above maintenance were not affected by treatment across all phases of production.

Serum Glucose Concentrations. Serum glucose concentrations were not affected by treatment or day (Figure 4.3A).

Serum NEFA Concentration. Serum NEFA concentrations were not affected by treatment (Figure 4.3B). There was an affect of day (74.52 ± 23.79 , 316.16 ± 24.52 , 151.82 ± 25.13 , and 91.15 ± 24.52 ng/mL for d 15, 29, 43 and 47, respectively; $P < 0.001$). Serum collected from sows approximately one week after farrowing (d 29) had the greatest NEFA concentrations, whereas gestating sows (d 15) had the lowest concentrations of NEFA.

Serum IGF-I Concentrations. There was an effect of day ($P < 0.001$) for serum IGF-I concentrations (46.59 ± 2.98 , 85.59 ± 3.04 , 97.91 ± 2.56 , and 104.06 ± 2.60 ng/mL for d 15, 29, 43 and 47, respectively; Figure 4.3C). There was no effect of treatment for d 15, 29 or 47. On d 43, the HS-TN-HS sows had the greatest serum IGF-I concentrations (116.11 ± 8.92 ng/mL; $P < 0.003$). The lowest concentrations of IGF-I on d 43 were found in TN-HS-TN (84.83 ± 8.92 ng/mL) and HS-HS-HS (89.52 ± 8.54 ng/mL) sows.

DISCUSSION

In this experiment, the metabolic response of sows to heat stress was studied. Sows experience changes in feed intake during phases of production. Typically, sows are limit fed in gestation and feed intake is fairly consistent. Limit feeding is practiced because obese sows have difficulty farrowing and may lactate poorly. During lactation,

sows are fed *ad libitum*, and feed intake increases dramatically in response to the increase in energy demand for lactation. After weaning, sows are fed based on body condition. Low body condition sows are offered more feed, and high body condition sows are offered less feed.

In this study, no differences were observed for feed intake for gestating sows (Figure 4.1A). Sows in HS chambers, however, gained less weight than sows in TN chambers during gestation (Chapter 3). One explanation for this may be that HS sows expended more energy in their attempt to thermoregulate under HS conditions. The TN sows did not have the same energetic requirement for thermoregulation. Our energy balance calculation did not include an estimate of ME for thermoregulation. The energy balance of the sows was the same (Figure 4.1B), although the sows were apparently different energetically based on their change in body weight.

Lactating sows increased feed intake after parturition (Figure 4.2A), and sows in HS-TN-HS had the greatest feed intake (Table 4.1). All sows under TN conditions consumed more feed (i.e., the sows in TN-TN-TN and HS-TN-HS consumed more feed than HS sows). Consequently, the TN sows produced more milk and had the heaviest pigs at weaning (Chapter 3). An obvious question that should be addressed is why did the TN treatment have greater feed intake? Heat stress causes lethargy, and the TN farrowing environment may have promoted an increase in feed intake because the sows were more active. Although activity level was not recorded, HS sows may have been less active and therefore did not stand as frequently to consume feed.

A second possibility is that the increase in body temperature experienced by HS sows had a direct effect on satiety centers in the hypothalamus. Behavioral changes that

occur in response to HS (panting, vasodilation, reduced activity, etc.) are coordinated by body temperature sensors located in the hypothalamus. This same area of the brain houses the satiety center (i.e., the part of the brain that controls feed intake). In all likelihood, feed intake is reduced during HS via the same integrated control that affects panting, vasodilation and activity. The consumption of feed creates a thermic effect, and it makes sense to increase satiety (reduce appetite) during HS. Sows in HS may have consumed less to reduce their own heat production.

A close examination of lactation feed intake reveals sows in TN-TN-TN, TN-HS-TN and HS-HS-HS experience a drop in feed intake between 4 and 6 days of lactation, whereas the HS-TN-HS seem to continue to consume more feed during this time. This suggests that there could be a metabolic mechanism through which sows that moved from HS gestation to TN farrowing had a greater appetite and consumed more feed when compared with sows that were in TN for the duration of the trial. The reason for the postpartum drop in feed intake is unknown. Sows in HS may have reduced appetite because of their environmental conditions, but this does not explain why the TN-TN-TN sows also showed a decrease in feed intake during the same period. It would also not explain how sows were capable of increasing feed intake after day 7 when they remained in the same environment. Previous studies have determined that feed intake for HS sows was less than TN sows but made no mention of the drop in feed during early lactation (Teague et al., 1968; Prunier et al., 1997; Renaudeau et al., 2001; Spencer et al., 2003). It can be speculated that the period in HS experienced by HS-TN-HS sows in gestation may have adapted their thermoregulatory mechanisms to the ensuing increase in heat production during lactation. This period of gestational HS essentially acted through an

imprinting mechanism to affect response to HS during lactation. In theory, all sows that start lactating experience a greater metabolic heat load and some form of thermal stress. The satiety, therefore, may be reduced as their body temperature increases postpartum (Chapter 3). Those sows that have been previously exposed to HS but are not in a TN environment do not reduce feed intake because their thermoregulatory mechanisms are primed during gestation. After weaning, however, feed intake decreased and there were no differences among treatments because sows were limit fed based on body condition (Figure 4.1A). Sows that were moved from HS farrowing to TN breeding consumed slightly more feed during breeding. Once again, there may be a metabolic mechanism stimulated by the change in environment that encouraged greater feed intake. Sows in HS-HS-HS continued to have decreased feed intake and consumed slightly less than the other sows.

Feed intake is a principle driver of energy balance. As mentioned above, there were no differences in feed intake during gestation. Energy balance was positive during gestation as well, and there were no differences among treatments (Figure 4.1B). Sows in HS-TN-HS had a slightly less positive energy balance even though feed intake was not different for these sows (Table 4.1). It is unclear why HS-HS-HS sows did not experience the same effect for energy balance because sows in HS-HS-HS were in the same gestation environment.

Energy balance after farrowing was initially negative for all treatment groups (Figure 4.2B) and then increased toward a positive plane for all sows until sows in TN-TN-TN, TN-HS-TN and HS-HS-HS dropped in feed take between days 4 and 6 of lactation. Energy balance during this period (d 4 to 6) followed the same pattern as feed

intake, and sows in most groups actually became more negative. The one exception was the sows in HS-TN-HS. As stated above, it is unclear why sows experience this drop in intake that ultimately impacts their energy balance.

Sows in HS-TN-HS were able to continue to move toward a positive energy balance during d 4 to 6, a period of lactation when other groups had faltered in terms of energy balance. By the second half of lactation these same sows were positive, whereas the TN-HS-TN and HS-HS-HS groups remained negative and TN-TN-TN sows were neutral to slightly positive. Based on the energy balance profiles, it appeared that this early period of lactation was important for determining longer-term energy balance during lactation. As stated above, the change in environment for the HS-TN-HS sows may have adapted them to the increase in heat production during lactation. This adaptation enabled a smoother transition toward metabolic heat production of lactation. All sows appeared to eventually adapt to greater heat production of lactation (Chapter 3), but this adaptation may have occurred too late to offset the short-term reduction in feed intake during early lactation. The energetics for this period were important in terms of sow productivity because sows in TN-TN-TN and HS-TN-HS produced more milk to subsequently wean the heaviest pigs (Chapter 3).

Energy balance was increasingly more positive after weaning (Figure 4.1B). One reason for the increase in positive energy balance was because sows were weaned and there were no requirements for lactation. Interestingly, sows in TN-HS-TN had the most positive energy balance during breeding (Table 4.1) because these sows consumed slightly more feed during breeding. There may be a compensatory mechanism that was initiated for these sows that stimulated feed intake when they came from HS farrowing to

TN breeding. This increase in feed intake for sows moving from a HS to a TN environment is reminiscent of the situation described in farrowing (sows moving from HS gestation to TN farrowing consumed more feed). Another interesting observation was that HS-HS-HS sows continued to consume less and had the most negative energy balance. This indicates that these sows may not be able to fully overcome and adapt to the effects of HS.

Metabolite concentrations are also controlled in part by feed intake. Serum IGF-I concentrations tended to increase as sows moved from gestation through farrowing and into breeding (Figure 4.3C). During gestation and breeding, treatment did not affect serum IGF-I. This perhaps reflects the fact that there were no differences among treatments for feed intake. The serum IGF-I on d 29 (1 wk after farrowing) was also similar. As previously discussed, sows had similar feed intake the first 4 days after farrowing, so no differences in IGF-I concentrations would be expected at this time. There were differences, however, the day before weaning (d 43). Sows that came from HS gestation to TN farrowing had the greatest concentration of IGF-I at the end of lactation. This treatment group had the greatest feed intake, indicating that the increase in IGF-I could perhaps be explained by the increase in feed intake. The sows in HS had the lowest concentrations of IGF-I, and these sows had lesser feed intake than TN sows. Other studies have also reported that undernourished sows have decreased concentrations of IGF-I (van den Brand et al., 2001; Hunter et al., 2004). This may be the first report showing that a treatment that stimulated feed intake can actually increase IGF-I concentrations in late lactation.

The HS-TN-HS sows, with the greatest concentrations of IGF-I, had larger follicles at weaning (Chapter 3). Blood concentrations of IGF-I are believed to be stimulatory to follicular growth through a synergistic effect on gonadotropins. Blood gonadotropin concentrations are reduced before weaning and their activity may be increased at the cellular level through the actions of IGF-I. Alternatively, the increase in feed intake may have increased gonadotropin secretion (theoretically LH, in this case), and this increase in LH may have led to an increase in follicular growth. Regardless, the follicular populations quickly normalized after weaning (Chapter 3) when IGF-I concentrations were also similar (Figure 4.3). Weaning leads to a large increase in LH secretion, and this stimulates follicular development. It also causes an increase in blood estradiol concentrations. The increase in blood estradiol concentrations along with the improved energy balance collectively increase blood IGF-I concentrations in sows after weaning.

The concentration of blood NEFA increased after parturition and then declined as lactation progressed (Figure 4.3B). There were no differences among treatments, but NEFA concentrations were dependent on day. After parturition, blood NEFA increased and tended to be greatest for sows that came from TN gestation to HS farrowing on d 29. This difference was not significant, but it is interesting to note that these sows gained more weight during gestation and potentially had more body reserves to mobilize. The increase in NEFA for all sows after farrowing suggests that these sows were mobilizing energy for milk production. The increase in NEFA postpartum was perhaps coordinated by the increase in GH that occurs in sows during lactation. As lactation progressed NEFA concentrations decreased perhaps because adipose tissue stores were depleted. Weaning

led to a further decrease in NEFA that coincided with lesser milk production and endocrine changes in the sow. Interestingly, blood glucose was not different among treatments or across days (Figure 4.3A). Apparently, the sow is fully capable of adapting to the glucose requirements for lactation and homostatically regulating her blood glucose.

To conclude, heat stress during lactation caused a decrease in feed intake. Sows in TN consumed more feed than HS sows with HS-TN-HS sows consuming the most feed. Subsequently, energy balance was more negative for sows with decreased feed intake. Sows in TN had a more neutral or positive energy balance toward the second half of lactation. These sows were able to produce more milk and wean heavier piglets (Chapter 3). Sows with greater feed intake had greater IGF-I at the end of lactation than sows with lesser feed intake. Sows in HS-TN-HS had the greatest concentrations of IGF-I and had larger follicles at weaning (Chapter 3). After parturition, NEFA concentrations were greatest with no effect of treatment. This indicates that sows were mobilizing body reserves to produce milk after they farrowed. Glucose was not different for sows across phases or treatments. Heat stress depressed feed intake to create a state of negative energy balance in lactating sows. Sows that consumed less feed had a greater negative energy balance and weaned pigs that were lighter. Depressed feed intake promoted less blood IGF-I and follicles that were smaller in size at weaning. Also, there may be a benefit when sows change environments. Feed intake increased and energy balance was more positive for sows that moved from HS gestation to TN farrowing. These sows also had greater follicular growth at weaning. Future studies should also focus on the effects of changing environments and how that affects the thermobiology of the sow, her productivity and her reproductive performance.

Table 4.1 Daily feed intake, ME_b, ME_M, requirements above maintenance and energy balance for sows in gestation, farrowing, and breeding.

	N	Treatment ¹						P < ²
		TN-TN-TN 15	TN-HS-TN 14	HS-TN-HS 14	HS-HS-HS 15	HS-HS-HS 15	Trt	
Feed intake, kg/d								
Gestation	2.3 ± 0.1	2.3 ± 0.1	2.3 ± 0.1	2.3 ± 0.1	2.3 ± 0.1	2.3 ± 0.1	NS	
Farrowing	3.6 ± 0.2 ^b	3.1 ± 0.2 ^c	4.0 ± 0.2 ^a	3.1 ± 0.2 ^c	3.1 ± 0.2 ^c	3.1 ± 0.2 ^c	0.001	
Breeding	1.7 ± 0.1 ^b	1.9 ± 0.1 ^a	1.7 ± 0.1 ^b	1.7 ± 0.1 ^b	1.5 ± 0.1 ^c	1.5 ± 0.1 ^c	NS	
Metabolizable energy intake (ME _i), Mcal ME/d								
Gestation	7.6 ± 0.2	7.6 ± 0.2	7.5 ± 0.2	7.5 ± 0.2	7.6 ± 0.2	7.6 ± 0.2	NS	
Farrowing	12.0 ± 0.6 ^b	10.6 ± 0.6 ^c	13.3 ± 0.6 ^a	10.5 ± 0.5 ^c	10.5 ± 0.5 ^c	10.5 ± 0.5 ^c	0.001	
Breeding	5.6 ± 0.4 ^b	6.2 ± 0.4 ^a	5.7 ± 0.4 ^b	5.1 ± 0.4 ^c	5.1 ± 0.4 ^c	5.1 ± 0.4 ^c	NS	
Metabolizable energy for maintenance (ME _M), Mcal ME/d								
Gestation	5.3 ± 0.1 ^c	5.3 ± 0.1 ^b	5.3 ± 0.1 ^a	5.3 ± 0.1 ^a	5.2 ± 0.1 ^d	5.2 ± 0.1 ^d	NS	
Farrowing	5.2 ± 0.1 ^c	5.3 ± 0.1 ^b	5.3 ± 0.1 ^a	5.3 ± 0.1 ^a	5.2 ± 0.1 ^d	5.2 ± 0.1 ^d	NS	
Breeding	4.9 ± 0.1 ^c	4.9 ± 0.1 ^b	5.1 ± 0.1 ^a	4.8 ± 0.1 ^d	4.8 ± 0.1 ^d	4.8 ± 0.1 ^d	NS	
Requirements above maintenance, Mcal ME/d								
Gestation	0.5 ± 0.1 ^c	0.5 ± 0.1 ^b	0.5 ± 0.1 ^a	NS				
Farrowing	9.7 ± 0.4 ^a	8.9 ± 0.4 ^b	9.3 ± 0.4 ^a	8.8 ± 0.4 ^b	8.8 ± 0.4 ^b	8.8 ± 0.4 ^b	NS	
Energy balance, Mcal ME/d								
Gestation	1.8 ± 0.2 ^a	1.8 ± 0.2 ^a	1.7 ± 0.2 ^b	1.7 ± 0.2 ^b	1.8 ± 0.2 ^a	1.8 ± 0.2 ^a	NS	
Farrowing	-2.9 ± 0.5 ^b	-3.6 ± 0.5 ^c	-1.4 ± 0.5 ^a	-3.6 ± 0.5 ^c	-3.6 ± 0.5 ^c	-3.6 ± 0.5 ^c	0.005	
Breeding	0.8 ± 0.4 ^b	1.3 ± 0.4 ^a	0.6 ± 0.4 ^b	0.6 ± 0.4 ^b	0.3 ± 0.3 ^c	0.3 ± 0.3 ^c	NS	

¹ The treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding.

²Overall type I error rate (P value) for treatment (Trt).
^{a,b, c} Treatment means having different superscript letters differ ($P < 0.05$; Duncan's multiple range test).

Table 4.2. Cumulative feed intake, ME_I, ME_M, requirements above maintenance and energy balance for sows in gestation, farrowing, and breeding.

	N	Treatment ¹						P< ²
		TN-TN-TN	TN-HS-TN	HS-TN-HS	HS-HS-HS	Trt	C1	
Cum. feed intake, kg/d		15	14	14	15	-	-	-
Gestation	45.7 ± 1.4	46.2 ± 1.5	45.3 ± 1.5	45.7 ± 1.4	NS	NS	NS	NS
Farrowing	81.8 ± 4.0 ^b	71.8 ± 4.0 ^a	90.6 ± 4.0 ^a	71.0 ± 3.8 ^b	0.003	NS	0.001	NS
Breeding	15.3 ± 1.1	16.6 ± 1.1	15.6 ± 1.1	13.8 ± 1.1	NS	NS	NS	NS
Cum. metabolizable energy intake (ME _I), Mcal ME/d								
Gestation	151.1 ± 4.6	152.6 ± 4.8	149.9 ± 4.8	151.1 ± 4.6	NS	NS	NS	NS
Farrowing	275.3 ± 13.4 ^{a,b}	241.7 ± 13.4 ^b	305.1 ± 13.4 ^a	239.1 ± 12.8 ^b	0.003	NS	0.001	NS
Breeding	50.6 ± 3.7	54.8 ± 3.7	51.4 ± 3.7	45.7 ± 3.6	NS	NS	NS	NS
Cum. metabolizable energy for maintenance (ME _M), Mcal ME/d								
Gestation	104.9 ± 1.2	105.6 ± 1.2	106.3 ± 1.2	104.7 ± 1.2	NS	NS	NS	NS
Farrowing	125.4 ± 1.8	126.1 ± 1.8	128.2 ± 1.8	124.7 ± 1.7	NS	NS	NS	NS
Breeding	43.9 ± 1.1	42.8 ± 1.1	45.7 ± 1.1	43.5 ± 1.1	NS	NS	NS	NS
Cum. requirements above maintenance, Mcal ME/d								
Gestation	100.0 ± 0.5	101.1 ± 0.5	101.1 ± 0.5	102.0 ± 0.5	NS	NS	NS	NS
Farrowing	219.9 ± 9.3	202.5 ± 9.3	213.4 ± 9.3	201.4 ± 8.9	NS	NS	NS	NS
Cum. energy balance, Mcal ME/d								
Gestation	36.2 ± 4.2	36.9 ± 4.4	33.6 ± 4.4	36.2 ± 4.2	NS	NS	NS	NS
Farrowing	-63.4 ± 10.4 ^b	-80.1 ± 10.4 ^b	-30.5 ± 10.4 ^a	-80.8 ± 9.9 ^b	0.004	NS	0.003	NS
Breeding	6.8 ± 3.2	12.0 ± 3.2	5.7 ± 3.2	2.2 ± 3.1	NS	0.096	NS	NS

¹ The treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C)

² Overall type I error rate (P value) for treatment (Trt) and individual treatment contrasts denoted as C1 (TN-TN-TN + TN + TN-HS-TN vs. HS-HS-HS + HS-HS-HS; sows in a thermoneutral breeding/gestation room vs. sows in a heat-stress breeding/gestation room), C2 (TN-TN-TN + HS-TN-HS vs. TN-HS-TN + HS-HS-HS; sows in a heat-stress farrowing room) and C3 (TN-TN-TN + HS-HS-HS vs. TN-HS-TN + HS-TN-HS; treatment interaction). ^{a,b}Treatment means having different superscript letters differ ($P < 0.05$; Duncan's multiple range test).

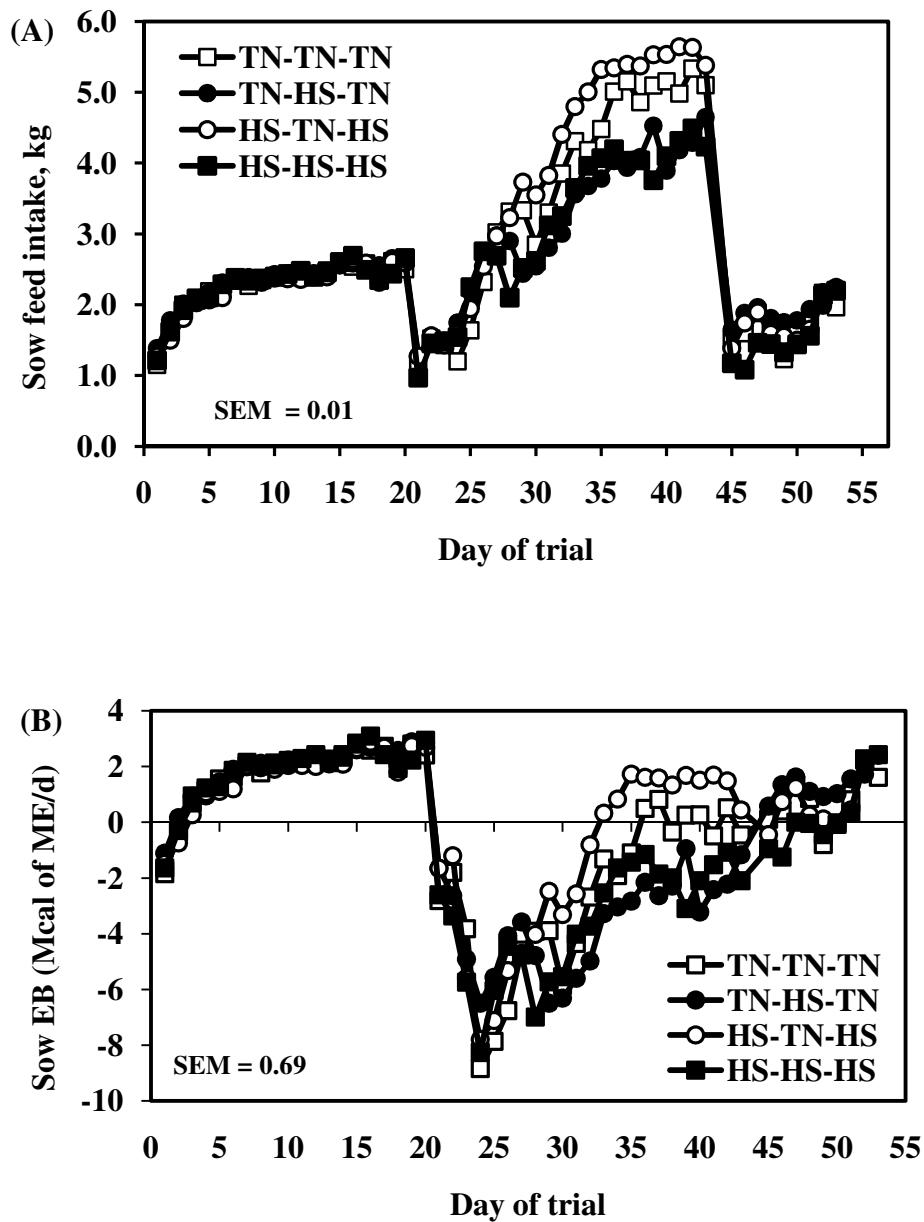


Figure 4.1. Least squares means for feed intake (A) and energy balance (B) of sows exposed to different ambient temperature treatments across 55 d of the trial. Treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding. Sows were in gestation from d 0 to 20, farrowing from d 20 to 44, and breeding after d 44.

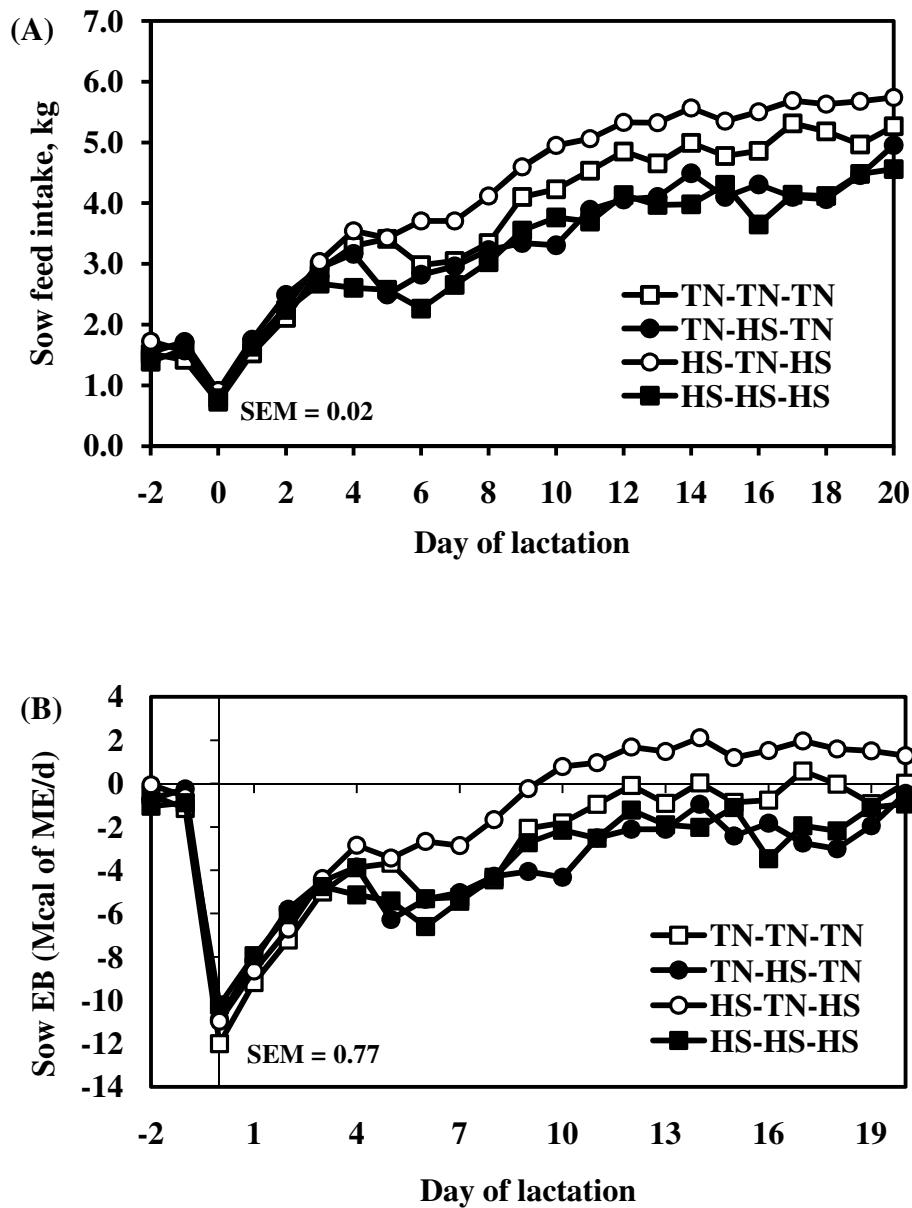


Figure 4.2. Least squares means for feed intake (A) and energy balance (B) of sows exposed to different ambient temperature treatments across d of lactation. Treatments are denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding. Sows were in gestation from d 0 to 20, farrowing from d 20 to 44, and breeding after d 44.

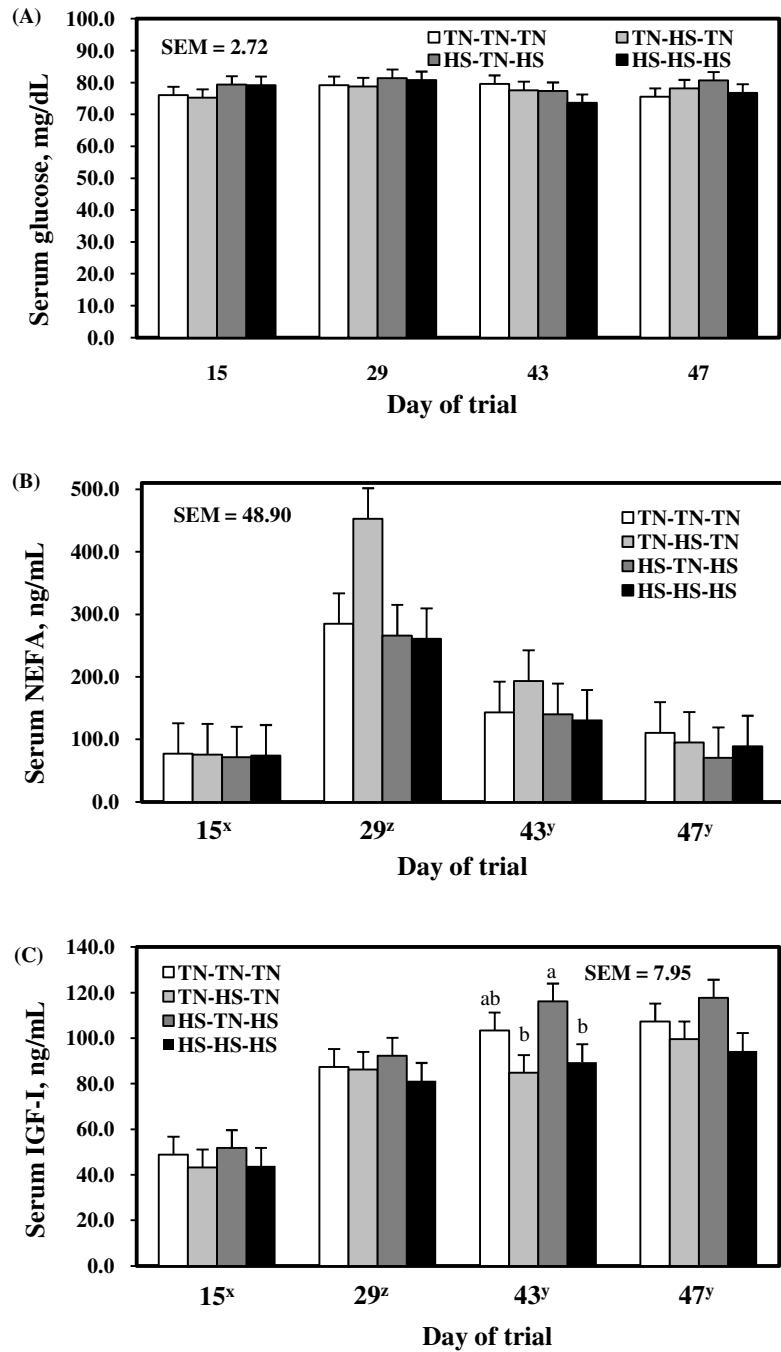


Figure 4.3. Least squares means for serum glucose (A) NEFA (B), and IGF-I (C) concentrations for sows at d 15 (during gestation), d 29 (after parturition), d 43 (day before weaning), and d 47 (three days after weaning during breeding). Sows were exposed to different ambient temperature treatments across 55 d of the trial denoted as TN-TN-TN, TN-HS-TN, HS-TN-HS or HS-HS-HS where the series of abbreviations represent the environmental temperature (TN; 18 to 20°C) or heat stress (HS; 24 to 30°C) that the sow experienced in gestation-farrowing-breeding. Sows were in gestation from d 0 to 20, farrowing from d 20 to 44, and breeding after d 44. ^{x,y,z}Means with different superscripts differ across day of trial ($P < 0.001$). ^{a,b}Within means, different superscripts differ ($P < 0.003$).

CHAPTER 5

CONCLUSIONS, IMPLICATIONS AND FUTURE DIRECTIONS FOR RESEARCH

CONCLUSIONS AND IMPLICATIONS

Heat stress during late gestation, lactation and breeding resulted in large changes in the thermal response of sows. The phase of production is a determinant of how elevated rectal temperature, respiration rate and skin temperature will be in response to heat stress. Increases in these measurements were observed from gestation to farrowing, as would be expected. Sows in lactation have increased energy intake and metabolic rate in order to produce an adequate amount of milk for their litters. This causes an increase in body heat increment. What is interesting, however, is the fact that when sows returned to breeding rectal temperature decreased, but sows did not achieve rectal temperatures as low as what was observed during gestation. Hypothetically, the sows biologically adapted to heat stress during lactation by changing their core body temperature set point. The change in respiration rate in response to heat stress was obvious across phases of production. Respiration rates for sows in HS gestation were greater and respiration rates further increased during lactation. The increase in respiration rate during lactation occurred as an effort by the sows to dissipate heat. Lactating sows have a greater heat increment as a result of increased feed intake and milk production. Increasing respiration

rates is one cooling mechanism used by sows. Weaned sows had decreased respiration rates that were lesser in breeding than in gestation. This reinforces the possibility that sows acclimated to the heat stress and reestablished their body temperature set point. Skin temperatures were greatest for HS sows across all phases. What is interesting about skin temperatures, however, is that HS sows in lactation experienced an immediate increase in skin temperature. Sows in TN had a slow increase in skin temperature that peaked during the last week of lactation. The immediate increase in HS sows indicates they were fully vasodilated early in lactation as a result of the necessity to dissipate heat as soon as possible. After weaning, skin temperature followed the same pattern as the other thermal responses and decreased, but HS remained greater than TN sows.

Feed intake was largely affected by heat stress during lactation. Differences in gestation and breeding were not determined as a result of limit feeding. Although feed intake was not different in gestation, sow body gain was greater for TN sows. The HS sows may have used the energy to dissipate heat rather than gain weight during late pregnancy. Thermoneutral sows consumed more feed in lactation while sows that came from HS gestation to TN farrowing consumed the most feed. This suggests that sows may be undergoing a metabolic transition that is triggered by the change in environment. Sows in TN-TN-TN and HS-TN-HS lost less body weight during lactation and also had a more neutral or positive energy balance. This led to greater milk production and the heaviest pigs at weaning. Interestingly, all sows except those in HS-TN-HS experienced a drop in intake by d 4 to 6 of farrowing that was associated with a more negative energy balance. The ability of these sows to continue to increase intake and continue toward a more positive energy balance may be explained by the ability to adapt their thermoregulatory

mechanisms. The sows had the opportunity to adapt to HS during gestation, and the adaption may have made it easier to acclimate to the increase in body temperature experienced during lactation. After weaning, sows that moved from HS farrowing to TN breeding consumed slightly more feed and had the most positive energy balance. These sows may have experienced a compensatory mechanism that stimulated feed intake and was similar to the mechanism described for sows in HS gestation and TN farrowing. Sows in HS-HS-HS had slightly less feed intake during breeding. This may be an indication that these sows were unable to fully adapt to and overcome the effects of HS.

Reproductive performance was not affected by treatment. Weaning-to-estrus intervals were well within industry standards for primiparous females. There was not a difference in the incidence of anestrus or the number of sows with silent ovulations. One possibility as to why a reduction in reproductive performance was not observed may be because the environmental center did not mimic the environment sows experience on a commercial farm as closely as preferred. The HS cycle may not have provided high enough heat stress, or the sows may have adapted. The cycle was the same each day, which is not the case on sow farms. Temperature cycles on farms are much more variable. There were also no differences observed for the second litter. This is interesting because it has been demonstrated that heat stress early in gestation causes decreased conception rates, increased embryonic death, and decreased farrowing rates. Once again, the sows may have been adapted to the HS once they returned to the breeding room or the HS cycle did not provide a high enough temperature to cause a detrimental effect. The sows may have left the trial too early and were not exposed to heat stress long enough during breeding. One other reason for the lack of differences in reproduction could be

because of photoperiod. Before sows started the trial they were housed at the University research farm. The gestation barn at the farm does not have windows and light is controlled by the farm manager. The photoperiod was much longer for the sows once they moved to the chambers, and this could have potentially masked an effect on reproduction that might have been observed.

Ovarian follicular growth was affected by treatment on the day of weaning with sows that moved from thermoneutral farrowing to heat stress breeding having slightly larger follicles. This may be attributed to the fact that these sows consumed more feed and had greater concentrations of IGF-I the day before weaning. This difference was short lived, however, as no differences in follicle size were observed by d 2 after weaning. This indicated that any effect treatment had on ovarian function was self corrected by the sow. From this perspective, there may be limited benefits of cooling sows during lactation.

FUTURE DIRECTIONS FOR RESEARCH

Future research should focus on understanding how sows have the capacity to adapt to heat stress and change their core body temperature set point. It may be beneficial to investigate the underlying biological mechanisms of this process. If this process is understood then this may determine how sows are managed during heat stress. More work should be done on why there seems to be limited benefits to cooling sows during lactation on ovarian follicular growth. Understanding how the environment during lactation affects follicular growth and how the sows may be able to compensate for detrimental effects of heat stress during that period should be further explored. Studies should also focus on the impact of changing environments and how that affects the sow

thermally, metabolically and reproductively. Developing a full understanding of these processes may allow for better management of sows in commercial production facilities.

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VITA

Amanda Williams was born in Oskaloosa, IA but spent the majority of her youth in Logansport, IN and was raised on a small sheep farm. She completed her undergraduate degree in 2005 with a BS in Animal Science from Purdue University. Upon graduation, Amanda pursued a career in the swine industry for two years. It was during that time period that her passion for pigs flourished. Amanda decided to continue her education with the intention of returning to the swine industry with a better understanding of pigs and more prepared to contribute to and improve swine reproduction. She will complete a MS in Animal Science/Reproductive Physiology with an emphasis in swine from the University of Missouri in August, 2009, under the guidance of Drs. Matthew Lucy and Timothy Safranski. Amanda has accepted a position in the swine industry with PIC in Hendersonville, TN.