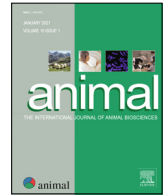




Contents lists available at ScienceDirect

# Animal

## The international journal of animal biosciences



### Review: What have we learned about the effects of heat stress on the pig industry?

F. Liu <sup>a,\*</sup>, W. Zhao <sup>b</sup>, H.H. Le <sup>b</sup>, J.J. Cottrell <sup>b</sup>, M.P. Green <sup>c</sup>, B.J. Leury <sup>b</sup>, F.R. Dunshea <sup>b,d</sup>, A.W. Bell <sup>e</sup>

<sup>a</sup> Research and Innovation Unit, Rivalea Australia Pty Ltd, Corowa, NSW 2646, Australia

<sup>b</sup> Faculty of Veterinary and Agricultural Sciences, University of Melbourne, Parkville, VIC 3010, Australia

<sup>c</sup> Faculty of Science, University of Melbourne, Parkville, VIC 3010, Australia

<sup>d</sup> Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, United Kingdom

<sup>e</sup> Department of Animal Science, Cornell University, Ithaca 14853-4801, USA

#### ARTICLE INFO

##### Article history:

Received 12 April 2021

Revised 24 June 2021

Accepted 25 June 2021

Available online xxx

##### Keywords:

Fetal development

Growth

Heat stress

Pig

Summer infertility

#### ABSTRACT

Pig production faces seasonal fluctuations. The low farrowing rate of sows mated in summer, increased carcass fatness of progeny born to the sows mated in summer, and slower growth rate of finisher pigs in summer are three economically important impacts identified in the pig industry. The purpose of this review is to examine advances over the past decade in understanding the mechanisms underlying the three impacts associated with summer conditions, particularly heat stress (HS), and to provide possible amelioration strategies. For impact 1, summer mating results in low farrowing rates mainly caused by the high frequency of early pregnancy disruptions. The contributions of semen DNA damage, poor oocyte quality, local progesterone concentrations, and suboptimal embryonic oestrogen secretion are discussed, as these all may contribute to HS-mediated effects around conception. Despite this, it is still unclear what the underlying mechanisms might be and thus, there is currently a lack of commercially viable solutions. For impact 2, there have been recent advances in the understanding of gestational HS on both the sow and foetus, with gestational HS implicated in decreased foetal muscle fibre number, a greater proportion of lighter piglets, and increased carcass fatness at slaughter. So far, no effective strategies have been developed to mitigate the impacts associated with gestational HS on foetuses. For impact 3, the slowed growth rate of pigs during summer is one reason for the reduced carcass weights in summer. Studies have shown that the reduction in growth rates may be due to more than reductions in feed intake alone, and the impaired intestinal barrier function and inflammatory response may also play a role. In addition, it is consistently reported that HS attenuates fat mobilisation which can potentially exacerbate carcass fatness when carcass weight is increased. Novel feed additives have exhibited the potential to reduce the impacts of HS on intestinal barrier function in grower pigs. Collectively, based on these three impacts, the economic loss associated with HS can be estimated. A review of these impacts is warranted to better align the future research directions with the needs of the pig industry. Ultimately, a better understanding of the underlying mechanisms and continuous investments in developing commercially viable strategies to combat HS will benefit the pig industry.

© 2021 The Authors. Published by Elsevier B.V. on behalf of The Animal Consortium. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

#### Implications

Summer conditions, particularly heat stress, compromise pig production efficiency. The low farrowing rate of sows mated in summer, increased carcass fatness of progeny born to the sows mated in summer, and slower growth rate of finisher pigs in summer are three known major impacts. The annual economic loss associated with these impacts in the pig industry is significant.

Research has progressed our understanding of the physiological impacts of heat stress, but the pig industry still requires commercially viable solutions on (1) mitigating the early pregnancy disruption of sows weaned and mated in summer; (2) improving foetal development of progeny born to the sows mated and gestated in summer, and; (3) increasing the growth rate of pigs finished in hot seasons.

\* Corresponding author.

E-mail address: [fliu@rivalea.com.au](mailto:fliu@rivalea.com.au) (F. Liu).

<https://doi.org/10.1016/j.animal.2021.100349>

1751-7311/© 2021 The Authors. Published by Elsevier B.V. on behalf of The Animal Consortium. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

## Introduction

Heat stress (HS) conditions in summer can compromise production efficiency and present a high cost to pork production globally. Reductions of reproductive performance in breeding herds and slowed growth rate in grower/finisher pigs are two typical impacts associated with HS. Heat stress can occur in pigs when the environmental temperature goes beyond their thermoneutral zones' upper limits. The physiological impacts of HS in pigs are comprehensive. Understanding and mitigating the physiological impacts of HS has been one of the key research topics of the past decade. Quantifying the impacts of HS in the pig industry is also important, because it helps research advances in the direction where the pig production is most limited by HS. Generalising the impacts of HS in global pig industry is challenging due to diverse climatic conditions, production systems, and market requirements. Reviewing the impacts of HS on the pig industry in a representative region is valuable for providing a more focused and in-depth analysis, and it creates opportunities to cross-validate and interpret the HS impacts using the knowledge generated from global studies. The impacts of HS in the pig industry are reviewed here using Australia, where its pig industry mainly under sub-tropical climate, as an example. The knowledge summarised in this review can be applied to the global pig industry where HS impacts are evident or emerging due to global warming.

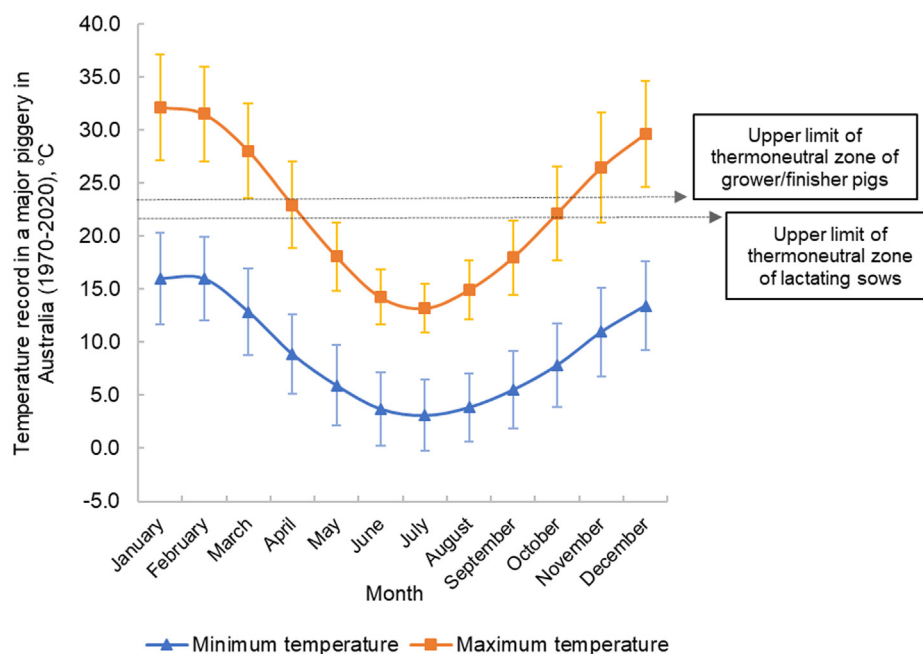
Many pig producers in Australia are located in sub-tropical regions, where considerable changes of temperature occur between seasons. High environmental temperature is one of the most critical features of summer in Australia. Fig. 1 illustrates the maximum and minimum temperatures in an intensive pig production region (Corowa, NSW, Australia, 35.99°S, 146.48°E) between 1970 and 2020. The average maximum temperature between November and March was above the upper limits of the thermoneutral zone for grower pigs (Huynh et al., 2005) and lactating sows (Quiniou and Noblet, 1999). Significant reductions in pig performance are usually anticipated during those months. Same as other regions that suffer from HS impacts, multiple research projects have been conducted in Australia to understand and mitigate

the impacts of HS on pig production with the funding support from the Pork CRC, Australian Pork Limited, Department of Agriculture, universities and other industry partners. The research conducted in sows has partially used a seasonal comparison design under natural conditions, due to the lack of climatically controlled research facilities and high sample sizes required, so the physiological impacts were related to summer conditions (hence include but are not limited to high environmental temperature). At the same time, there has been a considerable amount of climatically controlled experiments on the effect of HS on grower pigs. The current review's scope will focus on three major impacts that are reducing production efficiency in the pig industry – (1) increased reproductive failure of sows mated in summer, (2) increased carcass fatness of progeny of sows mated in summer, and (3) slower growth rate of finisher pigs in summer (Fig. 2). This review discusses each impact based on recent worldwide evidence, estimates the economic loss associated with these impacts, and summarises the solutions that have been evaluated. The current review aims to provide an updated research summary on the major impacts of HS on the pig industry and identify knowledge gaps for future research to improve the efficiency of pork production in these challenging and changing climatic conditions.

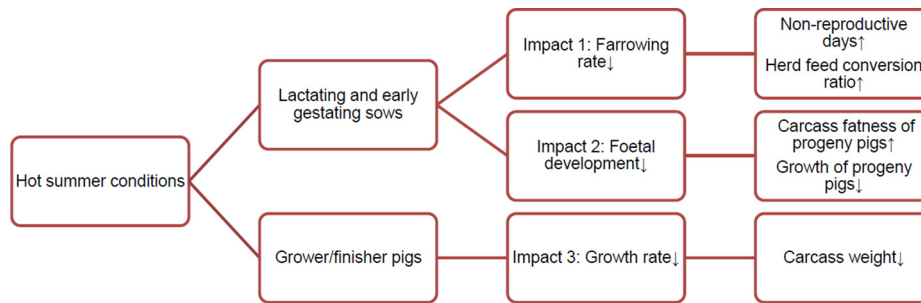
## Impact 1: Reduced farrowing rate of sows mated in summer

### Evidence for reduced farrowing rate of sows mated in summer

Reduced farrowing rate of domestic sows that were mated in summer remains a major issue in the global pig industry, including Australia. The common breeds used for terminal pig production in Australia are Large White- and Landrace-based genetics for the maternal line and Duroc-based genetics for the sire line (Department of Primary Industries, 2016). Recent production data (2010–2018) from two major Australian piggeries showed that the decline in the farrowing rate began in December. The average farrowing rate between December and March was 5% to 10% lower



**Fig. 1.** Temperature record of a major pig production region in Australia (1970–2020) (mean  $\pm$  SD). Data were retrieved from Corowa Airport weather station, NSW, Australia (35.99°S, 146.48°E; ID:074034, Bureau of Meteorology). The upper limit of the thermoneutral zone is defined as the environmental temperature when the pig starts to reduce total heat production (approximately 23 °C for growers (Huynh et al., 2005) and 22 °C for lactating sows (Quiniou and Noblet, 1999)).



**Fig. 2.** Three major impacts associated with summer conditions in pig production. First, the reduced farrowing rate of sows mated in summer increased the non-reproductive days and requires more sows to be mated for maintaining the supply of finisher pigs to the market, which inflates the herd feed conversion ratio. Second, for sows that manage to farrow after summer mating, a greater proportion of progeny is born with light BW ( $\leq 1.1$  kg) due to the impacts of gestational heat stress on foetal development. The increased proportion of born-light progeny pigs can result in inferior growth rate, reduced survival rate, and higher carcass fatness of the progeny population. Third, the slowed growth rate of pigs during hot conditions reduces carcass weight and consequently limits the revenue of pig producers.

than the annual average (Hermesch and Bunz, 2020). Recently published Australian commercial farrowing rates of sows mated in summer range from 64% to 83% which is lower than cooler months (89%) (Liu et al., 2019; 2020; Plush et al., 2019). The high environmental temperature coupled with the daylight length change is postulated to affect fertility in summer. An analysis of the farrowing records from a large Australian piggery between 2012 and 2017 found that if a high environmental temperature ( $>29$  °C) occurred 35 days before mating, it caused the largest reduction in farrowing rate (Bunz et al., 2019).

Farrowing success of sows relies on a series of events. Folliculogenesis results in oestrus and subsequent ovulation. Conception can take place when competent oocytes are fertilised by quality sperm. Maternal recognition of pregnancy triggers endocrine changes and the preparation of the uterus to facilitate embryo implantation (Spencer and Bazer, 2004). The progesterone secreted from functional corpora lutea plays an important role in the maintenance of pregnancy. Summer infertility mainly manifests as an increased proportion of sows that have an irregular return after mating, and thus an increased number of matings are required to establish a viable pregnancy. Data from Australia show the total number of piglets born per litter and the number of piglets born alive both remain constant among seasons (Lewis and Bunter, 2011). In the past 40 years, improved understanding of the physiological mechanisms behind summer infertility and developing intervention strategies have been a critical research focus (King, 2017). In the last 5 years, the consensus of summer infertility studies has been that the reduction in the farrowing rate of sows mated in summer is mainly due to early pregnancy disruption rather than a failure to conceive.

#### Altered oestrus-to-ovulation interval during summer mating

Pig producers usually schedule artificial insemination (AI) based on the detection of behavioural oestrus, so knowing the accurate oestrus-to-ovulation interval (OOI) is essential for scheduling AI to achieve optimum conception. There are conflicting findings on OOI during HS conditions. A climatic controlled study found that HS during lactation (31 °C, 8:00–16:00; 26 °C 16:00–8:00) reduced follicle size from 6.7 to 5.8 mm and prolonged OOI from 1 to 2.5 days (Cabezón et al., 2017). Conversely, OOI was 10 hours shorter in sows whose litters were weaned in summer than winter (21.8 h vs 31.4 h) (van Wettere, 2013). Similarly, the sows lactated and mated under summer conditions (December 2019–March 2020;  $25.4 \pm 5.01$  °C mean  $\pm$  SD; Australia) had an average OOI of 1.1 days (Liu et al., 2021a). The conflicting findings between studies may be due to different environmental conditions or genotypes. Notably, even if changes in OOI are evident in sum-

mer, the timing and success of conception are unlikely to be affected due to a mistimed mating or insemination, when a double AI programme is used (i.e.: 1st AI at the first detectable behaviour oestrus after weaning and 2nd AI at 24 h after this). Insemination at the onset of oestrus remains the best timing for mating weaned sows with such an OOI (1.1 days) in summer because insemination performed at 0–24 h before ovulation can achieve optimum sow conception rates (Kemp and Soede, 1996). Interestingly, the farrowing rate of the sows with an average OOI of 1.1 days that received two AIs in summer remained low (65%) (Liu et al., 2021a). Hence, factors during early pregnancy (before day 35), including maternal recognition of pregnancy, embryo survival, uterine environment, and sperm as well as oocyte quality, may be responsible for lower farrowing rates and are discussed in the next section.

#### Role of semen and oocyte quality in summer infertility

Boar fertility contributes to the reduced farrowing rate of sows mated in summer. The impacts of hot conditions on boar fertility were reported as reduced sperm concentrations, increased percentage of abnormal sperm, and decreased sperm motility (Stone, 1982; Huang et al., 2000; Zasiadczyk et al., 2015). The reduced concentration of sperm in ejaculates implies a reduced number of matings can be achieved, as semen is usually diluted to a constant number of viable sperm cells per dose before being used in commercial pig production. The reduction in sperm motility means fewer sperms can reach the oviduct to fertilise oocytes and thus, the conception rate may be lower. The motility of sperm in the ejaculates of Large White boars reduces when the air temperature increases above 30 °C (Stone, 1982). Exposing boars to hot conditions (31–35 °C) for 90 days reduced sperm motility, reduced percentage of pregnant gilts by day 30 of gestation from 41% to 29%, and reduced embryonic survival from 71% to 49% by day 30 of gestation (Wettemann et al., 1976).

A recent study showed tropical conditions can cause DNA damage (or known as DNA fragmentation) without affecting sperm motility. Specifically, humid tropical conditions ( $29.2 \pm 0.2$  °C;  $71.4 \pm 1.2\%$  relative humidity; mean  $\pm$  standard error; in North Queensland, Australia) reduced the concentration of sperm by 62% and increased the percentage of spermatozoa with DNA damage from 1 to 16% in Large White boars although sperm motility was not affected (Peña et al., 2019a; 2019b). By comparison, DNA damage in semen was not different among seasons in a European study (Zasiadczyk et al., 2015). The disparity of the results may be due to genotypic, geographic, and climatic differences. The semen with normal motility may still be able to fertilise eggs, but the DNA damage can promote embryo arrest and apoptosis

(Alvarez Sedó et al., 2017). A meta-analysis identified that the high DNA damage in sperm was associated with an increased likelihood of abortions in humans (Robinson et al., 2012). Similar extensive studies on elucidating effects of semen DNA damage on conception rate are yet to be undertaken in pigs but highlight an urgent area for future research.

Oocyte quality is also a major factor that determines fertilisation success (Krisher, 2004). Oocyte quality, measured as the ability of oocytes to form blastocysts, was inferior in sows weaned in summer compared with winter (Bertoldo et al., 2010). Yet such a seasonal effect was not evident in the oocyte quality measured in gilts (van Wettère, 2013), implying that the oocyte quality may be associated with impacts from summer lactation. The number of pre-ovulatory follicles postweaning and the progesterone concentration in the follicular fluid (stratified by follicle size) were lower in sows weaned in summer than winter (Bertoldo et al., 2010, 2011). Also, follicle fluid collected from sows lactated and weaned in summer displayed metabolites that implied that the oocytes may become susceptible to oxidative stress (Bertoldo et al., 2013). Oxidative stress can impair oocyte maturation and reduce fertilisation rate (Tamura et al., 2008). In addition, poor oocyte quality is known to cause embryonic loss during early pregnancy (Hunter, 2000). Taken together, the inferior oocyte quality in the sows weaned in summer, together with the DNA damage in sperm, may partially explain the increased early pregnancy disruptions.

#### Strategies to improve semen and oocyte quality

Antioxidant supplements have shown beneficial effects in mitigating the negative impacts of HS on semen quality. For example, supplementation of an antioxidant mixture to boars for 42 and 84 days reduced DNA-damaged sperm from 16% to 10% and 7%, respectively, during summer, although sperm concentration and motility were not improved (Peña et al., 2019a; 2019b). Vitamin C or D supplementation above the normal recommended levels improved the semen quality of boars in summer (Lin et al., 2017; Lugar et al., 2019). The entire spermatogenic process in boars takes approximately 45 days (Parrish et al., 2017), which makes the impacts of HS on semen quality longer than the actual hot period. Therefore, the duration of antioxidants supplementation should be extended by several weeks after the hot period.

The strategies that reduce impacts of HS in lactating sows may have implications for oocyte quality and thus subsequent reproductive performance. Betaine, trimethyl-glycine, can protect cells from osmotic stress and convert homocysteine to methionine (Hammer and Baltz, 2002). These features make it a possible nutritional supplement to reduce the negative effects of HS. Betaine supplementation (0.22%) during a hot lactation (31 °C for 8 h and 26 °C for 16 h) increased follicle development of sows (Cabezón et al., 2017). A recent study showed that 0.2% betaine supplementation during summer lactation (25.4 ± 5.01 °C for mean ± SD) numerically increased subsequent farrowing rate by 6% (Liu et al., 2021a). Another group of candidates for improving oocyte quality are essential fatty acids. Specifically, a study suggests that 10 g/day  $\alpha$ -linolenic acid (*n*-3) and 125 g/day linoleic acid (*n*-6) are required for modern lactating sows to achieve an optimum subsequent pregnancy retention rate (Rosero et al., 2016). These two fatty acids are not only energy substrates for oocyte maturation but also serve as precursors for prostaglandins that are important for uterine health postpartum, follicle development, and ovulation (Wathes et al., 2007). However, it is likely these two fatty acids can be depleted in modern, prolific, lactating sows due to a negative energy balance during summer (Rosero et al., 2016), thus supplementation may be required. Insulin-like growth factor 1 plays a role in facilitating follicle development (Giudice, 1992),

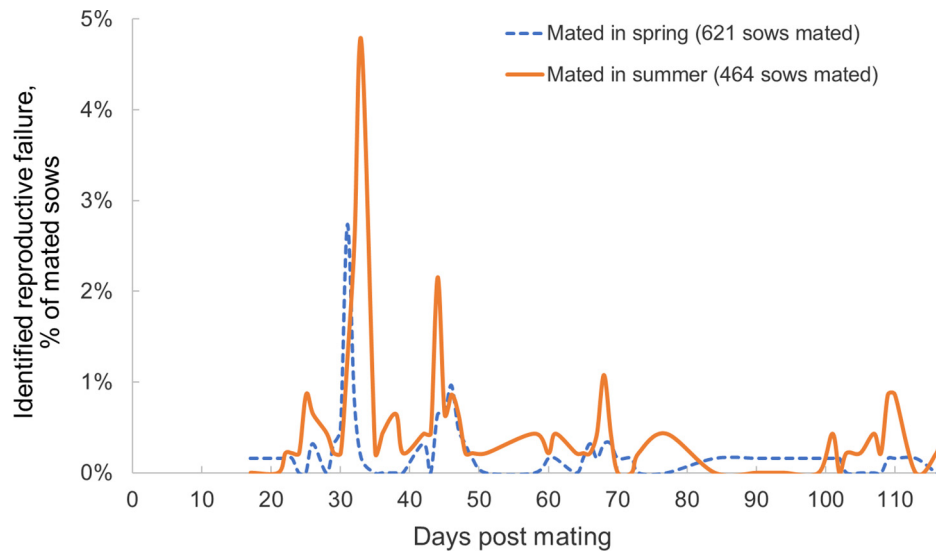
and thus glucose supplementation during weaning-to-oestrus interval has been studied due to its effects in stimulating IGF-I. A recent study showed that a 5% dextrose supplementation (equivalent to 200 g dextrose per sows per day) during weaning-to-oestrus interval tended to increase farrowing rate (av. 64%) by 5.9% in the sows mated in summer (Plush et al., 2019).

#### Early pregnancy loss is the major manifestation of summer infertility

Early pregnancy losses of sows mated in summer is a major manifestation of summer infertility reported in Australia and Europe (Love et al., 1993; Tast et al., 2002). A recent study conducted in an Australian commercial piggery again confirmed that sows mated in summer predominantly exhibited pregnancy loss before day 35 of gestation compared with those mated in cool months (Liu et al., 2021a). Fig. 3 illustrates the percentage of sows identified as having the reproductive failure on an Australian farm with summer infertility. The percentage of regular return (visually identified using behavioural signs between 17 days and 22 days post-mating) was not the major contributor to the low farrowing rate of sows mated in summer (January–March), indicating conception was not the major issue. Pregnancy checks were conducted at 28, 42, and 63 days postmating. A major peak in reproductive failure was identified before 35 days postmating (between the day 28 and day 42 pregnancy check), suggesting that the disruption occurring during early gestation was the primary cause for the low farrowing rate of the sows mated in summer. In addition to the role of sperm DNA damage and inferior oocyte quality in embryo loss discussed above, a growing body of evidence supports that an inappropriate maternal recognition of pregnancy signal likely contributes to pregnancy loss before d 35 of gestation (discussed below).

Corpora lutea (CL) function, namely progesterone production, modulates the uterine environment and embryo development (Vallet et al., 1998). Thus, many previous studies hypothesised that summer conditions interrupt progesterone secretion, impairing embryo development during early gestation, but results showed that progesterone concentration was not affected or was even increased by hot conditions. Exposing gilts to cyclic HS conditions (31.6 °C 12 h per day; 21–31% relative humidity) for 11 days post-oestrus reduced the average weight of CL by 15% but did not affect the progesterone concentration in blood or luteal tissue in a US study (Bidne et al., 2019). Similarly, blood progesterone concentrations monitored over the first six weeks of gestation were similar between pregnant sows mated in a European summer-autumn and those mated in winter-spring (Tast et al., 2002). In contrast, a seasonal comparison study showed that plasma progesterone concentration increased more rapidly 72 hours after oestrus detection during an Australian summer than winter (van Wettère, 2013). Therefore, the hypothesis that a reduction in progesterone concentration is associated with a reduced farrowing rate should be re-evaluated. Perhaps future studies need to look at the oestrogen to progesterone ratio, known to be crucial in regulating the reproductive tract (Edgerton et al., 2000), not simply a change in progesterone concentration.

Uterine endometrial preparation and signalling are required for successful implantation. Still, it is unknown whether HS during lactation, weaning-to-oestrus interval, and early gestation can affect this process in sows. In dairy cows, early embryo loss in cows mated in summer may be a consequence of increased prostaglandin F2 alpha (PGF<sub>2 $\alpha$</sub> ) secretion (Putney et al., 1988). PGF<sub>2 $\alpha$</sub>  is a luteolysin that can cause luteal regression and thus interfere with progesterone secretion required for embryo implantation and maintenance. Future research should investigate whether HS triggers this abnormal increase or changes in the secretion of PGF<sub>2 $\alpha$</sub>  or



**Fig. 3.** Identified reproductive failure in an Australian piggery with summer infertility. Visual assessment on regular returns (oestrus) was conducted between 17 and 22 days postmating. Routine pregnancy check was conducted using transabdominal ultrasound scan at 28, 42 and 63 days postmating. The farrowing rate for sows mated in August–October (spring) and January–March (summer) was 88% and 76%, respectively. Farrowing rate between the two seasons significantly differed ( $P < 0.001$ ; Chi-squared analysis).

PGE, the protective prostaglandin secreted by sows during early gestation.

A biphasic pattern of oestrogen secretion from conceptuses is required for pregnancy establishment in pigs. Specifically, oestrogen is secreted from the elongated blastocyst into the uterine lumen at around 11–12 days of pregnancy (Geisert et al., 1982), which is believed to redirect endometrial secreted  $\text{PGF}_{2\alpha}$  from the uterine vascular into the lumen, to avoid its ability to cause luteolysis. Further oestrogen secretion by the conceptus on days 14–18 of pregnancy (Geisert et al., 1990) is essential for embryonic survival from day 24 of pregnancy onwards in pigs (Meyer et al., 2019). For future experiments, a hypothesis to be tested is whether HS may reduce embryonic development and oestrogen secretion, thus increase pregnancy loss before day 35 of gestation in sows mated in summer. Future experiments studying the effects of HS on conceptus oestrogen secretion from conceptuses in gestating sows may elucidate the mechanism of early embryo loss in sows mated in summer.

#### Solutions to reduce early pregnancy loss of sows mated in summer

Solutions to reduce the early pregnancy loss are more relevant to the summer infertility issue in the pig industry, given the peak of reproductive failure occurs before 35 days of gestation. The key factor causing the early pregnancy disruption remains unclear which creates difficulty for developing targeted intervention strategies. In addition to semen and oocyte quality, other factors including uterine preparation, maternal pregnancy recognition, and embryo survival should be considered. A study determined that an injection of 1000 IU human chorionic gonadotropin (hCG) 12 days after mating increased blood oestrogen and progesterone concentrations, and improved conception and farrowing rates in primiparous sows mated in summer (Seyfang et al., 2016). It is likely that the hCG induced ovulation of smaller follicles, which resulted in additional CL to produce more progesterone and oestrogen to support endometrium and embryonic growth. An alternative to a hormone intervention is the addition of micronutrients in the diet to improve reproductive outcomes. A study showed that increasing dietary vitamin B12 (150–300  $\mu\text{g}/\text{kg}$ ) and folic acid (from 5 to 25  $\text{mg}/\text{kg}$ ) just after conception reduced the early preg-

nancy loss (<30 days postmating) from 7% to 3% (van Wettere et al., 2013).

Management strategies such as reducing aggression during early gestation for sows that mated in summer should also be evaluated. Our recent study identified that sows mated in summer, then housed in the group pens, had increased aggression during early gestation which coincided with the low farrowing rate (Liu et al., 2020). Reasons for the high aggression remain unknown but, in part, may be due to either high temperature altering sow behaviour and/or increased fighting to access feed for recovering lactational weight loss. A European study found that loose group-housed gestating sows are more likely to return to oestrus than those individually housed in stalls (Peltoniemi et al., 1999). Most gestating sows are loose-housed in Australia, due to animal welfare requirements, so strategies to reduce aggression of group-housed gestating sows that mated in summer should be investigated, particularly in the feeding system where the social hierarchy determines feeding order. Preliminary results from an ongoing study showed that reducing the group size of gestating sows from 40 to 20 in the pen equipped with an electronic sow feeder reduced the number of skin injuries and reduced early pregnancy loss from 19.1% to 5.5% during summer (Smith et al., 2021). However, it remains unclear whether it was the increased floor space or feeder space that contributed to the reduction of early pregnancy loss.

#### Impact 2: Impacts of summer condition during early gestation on progeny fat composition

##### “October Fat Pigs” phenomenon in Australia

Carcass backfat thickness peaks annually around October (late winter and spring) in Australia (Trezona et al., 2004), giving rise to the phenomenon of “October Fat Pigs”. Similar seasonal patterns of carcass fatness have also been reported in South Korea (Choi et al., 2019) and Spain (Rodríguez-Sánchez et al., 2009). An increase of backfat in the Australian market (e.g.: above 12 mm) can reduce the carcass value by 10–20%. The pigs that contributed to the seasonal increase of carcass backfat are the progeny born to the sows mated in summer who also usually experience summer conditions during lactation and the subsequent early gestation. Therefore, HS during those two stages possibly affected foetal

**Table 1**  
Effects of gestational heat stress on carcass fatness of progeny pigs.

Studies	Thermal exposure of sows	Litter size	Birth weight	Progeny environment	Growth performance	Carcass fatness
Boddicker et al. (2014)	28–34 °C, first half gestation	→	→	Thermoneutral until 12 weeks	ADFI→ ADG→ G: F→	Backfat↑17%
Boddicker et al. (2014)	28–34 °C, second half gestation	→	→	Thermoneutral until 12 weeks	ADFI→ ADG→ G: F→	Backfat→
Johnson et al. (2015a)	27–35 °C, whole gestation	→	↓17%	Thermoneutral until 60 kg	ADFI→ ADG→ G: F→	Lipid%→
Johnson et al. (2015b)	28–34 °C, whole gestation	NA	NA	Thermoneutral until 80 kg	ADFI→ ADG→ G: F↓14%	Lipid gain↑32%, Protein gain↓11%
Cruzen et al. (2015)	28–34 °C, whole gestation	→	→	Thermoneutral until 110 kg	ADFI↑12% ADG→ G: F→	Backfat→
Serviento et al. (2020)	28–34 °C, days 9–109 gestation	NA	NA	Thermoneutral until 104 kg	ADFI→ ADG→ G: F→	Backfat→ Perirenal fat%→
Serviento et al. (2020)	28–34 °C, days 9–109 gestation	NA	NA	Heat stress 28–34 °C from 84–140 days age	ADFI→ ADG→ G: F→	Backfat→ Perirenal fat%→ Lean meat%↓2%
Tuell et al. (2021)	28–36 °C, days 11–59 gestation	NA	NA	Thermoneutral until 117 kg	NA	Backfat→ Perirenal fat%→ Loin area↓10%

Abbreviations: → = unchanged; ↑ = increased; ↓ = reduced; NA = data not available; ADFI = average daily feed intake; ADG = average daily gain; G:F = gain: feed.

development and muscle deposition potential. While, there is little evidence demonstrating that lactational HS can affect subsequent foetal development, that progeny born to sows mated in summer were fatter is consistent with emerging research on impacts of gestational HS on progeny adiposity (Table 1). Two climate-controlled studies have observed that gestational HS increased fat deposition of progeny pigs (Boddicker et al., 2014; Johnson et al., 2015b).

It remains unclear whether the impacts of gestational HS are universal on all foetuses or expressed as an increased percentage of piglets born light. A climate-controlled study showed that HS over the entire gestation reduced birth weights (Lucy et al., 2012), whereas other smaller studies showed similar birth weights between thermoneutral and heat-stressed gestating sows (Boddicker et al., 2014; Bernhard et al., 2020). Sows mated in Australian summer had a greater proportion of born-light piglets ( $\leq 1.1$  kg) than sows mated in autumn (24.2% vs 15.8%), and this is estimated to increase the average backfat thickness by 0.33 mm in the progeny population (Liu et al., 2020). The reduced birth weight from the summer matings was unlikely to be due to a reduction of gestational feed intake because gestating sows were restricted fed to a common amount regardless of the season. Impacts of gestational HS on placental efficiency and foetal development are probably involved, and these two impacts are discussed below.

#### Effects of gestational heat stress on placental insufficiency

The placenta is the primary interface between the dam and foetus, providing oxygen and nutrients to support foetal development, but also synthesising chorionic hormones to maintain pregnancy and foetal development (Fowden and Forhead, 2009). The relationship between HS, placental insufficiency, and impaired foetal development has been established in sheep (Bell et al., 1987), but is poorly characterised in the sow. A recent experiment quantified the effects on placental development of exposing pregnant gilts to 33 °C between days 40 and 60 of gestation (Zhao et al., 2020), and found that HS increased placental surface area and mass, but this was not in conjunction with an increase in foetal size or weight. This morphological measurement indicated a placental insufficiency

caused by gestational HS. Analysis of placental gene expression showed that HS reduced the expression of two nutrient transporters - glucose transporter 3 and cationic amino acid transporter 1 (Zhao et al., 2020). The increased placental hyperplasia observed by Zhao et al. (2020) likely reflected a compensatory adaptation to overcome the reduction in placental nutrient transport capacity. However, a recent study that used a higher magnitude of HS during the second month of gestation did not affect the placental weight or the ratio between placental weight and piglet birth weight (Bernhard et al., 2020). Reasons for the inconsistent effects of HS on placental development in gestating sows remain unclear.

The mechanisms underlying effects of HS on conceptus development in pigs have not been studied. However, numerous studies on heat-stressed pregnant ewes have been reviewed recently (Limesand et al., 2018). These include observations of reduced uterine blood flow associated with heat-induced redistribution of maternal cardiac output away from visceral organs to enable heat dissipation in the skin and decreased placental expression of transporters for glucose and amino acids. There is no doubt that retardation of placental growth is associated with decreases in uterine and umbilical blood flows in late pregnancy, and that these effects could influence the flow-limited placental transfer of some nutrients (Bell et al., 1987). However, it is less certain that altered uteroplacental flows are a primary cause rather than a consequence of HS-induced placental growth. In the sheep, HS-induced placental growth retardation is evident by mid-gestation, well before any discernible effect on foetal growth (Vatnick et al., 1991). The fact that this stunting was due to inhibition of placental hyperplasia is consistent with the direct effect of HS on growth retardation in other highly proliferative cell types, including male and female germ cells (Setchell, 1998; Khan et al., 2020).

#### Gestational heat stress reduces foetal muscle fibre development

Emerging studies have focused on the impacts of gestational HS on proliferative growth of muscle because of its potential association with postnatal carcass composition - an economically impor-

tant trait in the pig industry. Although muscle fibres were the same size on average between HS and thermoneutral treatments, there were approximately 15% fewer skeletal muscle fibres in the M. *Longissimus* on day 60 of foetuses from gilts housed at elevated temperatures between days 40 and 60 of gestation (Zhao et al., 2020). Similarly, the rate of skeletal muscle myogenesis, myofibre numbers, myoblast proliferation, and myofibre size was reduced in the foetuses from the sheep that were exposed to HS (Yates et al., 2014; Chang et al., 2020). Skeletal muscle growth is driven by hyperplasia and hypertrophy which happens during the foetal phase and postpartum phase, respectively. The reduced number of muscle fibres implies that there are comparatively fewer fibres to undergo hypertrophy as the animal matures. Furthermore, the muscle fibres of the foetuses from gilts exposed to elevated temperatures had fewer myonuclei numbers (Zhao et al., 2020). This reduces each fibre's transcriptional efficiency and presents a limitation to hypertrophic growth. Therefore, the results of Zhao et al., (2020) indicate that gestational HS would inhibit muscle accretion by inhibiting both muscle fibre hyperplasia and the potential for later hypertrophy. Skeletal muscle protein accretion was reduced in foetal sheep by maternal heat stress (Rozance et al., 2018).

#### *An interaction of postnatal environment and birth weight on carcass fatness*

The phenotype of increased carcass fatness is the consequence of impaired muscle fibre proliferation and likely due to a high level of energy intake during the postnatal environment. Impaired muscle fibre proliferation can reduce the lean tissue deposition potential later in life (Alvarenga Dias et al., 2012). The progeny born to the sows mated in summer usually finishes in late winter and early spring, and the relatively cool environmental temperature ensures high voluntary energy intake. More energy intake would have to be deposited as fat when the lean tissue deposition potential is reduced. In support of this, born-light piglets (<1.1 kg) had increased backfat at 100 kg live weight in spring versus summer. The higher energy intake during late winter and early spring likely resulted in higher fat deposition in the born-light pigs. By comparison, the piglets with normal weight (1.3–1.7 kg range) had similar backfat thickness at 100 kg live weight despite different energy intake during the finishing seasons (Liu et al., 2020). This implies that the high energy intake due to the cool finishing season exacerbated carcass fatness in born-light piglets, but the born-normal piglets can deposit lean and fat tissue at a constant ratio over a wider range of energy intakes. Collectively, the increased carcass fatness observed in late winter and early spring is a consequence of a higher proportion of born-light progeny, with the voluntary energy intake further beyond their muscle deposition potential.

#### *Lack of strategies to reduce gestational heat stress impacts on foetal development*

The impacts of gestational HS on placental and foetal development, and progeny fat deposition in pigs are the emerging research topics, thus no mitigation strategies have been developed. Little is known about how placental and foetal development could be improved in heat-stressed sows. As the increased proportion of born-light piglets can contribute to the increased carcass fatness in late winter and spring, developing strategies to improve piglet birth weights and reduce the percentage of light piglets that are born to the sows mated in summer may be a temporary goal before we can target the specific mechanism of the impacts of gestational HS on foetal development. The nutritional strategies that can improve piglet birth weight may counteract the negative impacts associated with gestational HS. In a recent study, we found increas-

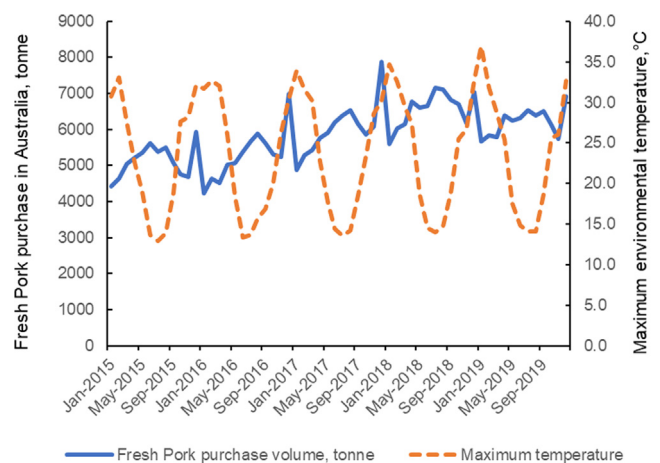
ing the feed allowance from 2.6 to 3.5 kg during the 0–30 days of gestation after summer lactation can improve average piglet birth weight and reduce the percentage of born-light piglets but at the cost of reduced litter size (Liu et al., 2021b). The reduction in the proportion of born-light piglets may improve the overall growth performance and reduce carcass fatness in progeny populations. More mitigation strategies should be investigated when our understanding of how gestational HS impacted foetal development has progressed.

### **Impact 3: Impacts of heat stress on growth performance of grower/finisher pigs**

Reduced growth rate of grower/finisher pigs during the hot season is a common issue in the pig industry worldwide. Australian data suggested that the feed intake and growth rate of finisher pigs are 8% lower in summer than in cool seasons (Lewis and Bunter, 2011). Pork consumption in Australia peaks in December (Fig. 4), which coincides with the start of summer in the Southern Hemisphere. Carcass weight usually reduces in summer due to the slowed growth rate in addition to younger slaughter age. The high volume of pork sold during summer can magnify the economic loss due to the reduced carcass weight. Reduced feed intake is a major reason for the slowed growth rate of grower/finisher pigs under hot conditions. Research in the past decade explored the direct impacts of HS in intestinal barrier function, inflammatory response, and postabsorptive metabolism. These direct impacts of HS may also play a role in affecting growth performance and carcass composition.

#### *Reduced feed intake and growth rate of finisher pigs*

The inhibitory effect of high environmental temperature on feed intake of grower/finishers is well researched. For example, Huynh et al., (2005) found every degree increase in environmental temperature above 23 °C reduces feed intake of grower pigs by 89–106 g, depending on humidity. Feed efficiency (gain: feed) is less influenced by hot conditions. For example, a recent meta-analysis showed that hot conditions (29–35 °C) did not affect gain: feed ratio (da Fonseca de Oliveira et al., 2019). An early meta-analysis showed that gain: feed was only slightly reduced during extremely hot conditions (30–36 °C) (Renaudeau et al., 2011). Therefore, the reduction in feed intake is a major factor that reduces growth rate



**Fig. 4.** Volumes of fresh pork purchase in Australia between 2015 and 2019. The peak of fresh pork consumption in Australia coincides with the hot months. Data on fresh pork purchase volume were provided by Australian Pork Limited. Data on maximum environmental temperature were recorded near a major pork-producing region in Australia (Corowa, NSW, Australia, 35.99°S, 146.48°E; Weather station ID:074034, data from Bureau of Meteorology of Australia).

and consequently carcass weight in hot conditions. It is generally acknowledged that the avoidance of feed thermic effect and heat production are the causes for the reduced feed intake of pigs during hot conditions.

#### *Solutions to improve growth rate of finishers during summer*

Dietary modifications have been studied as a strategy to mitigate the impacts of HS on growth performance. Reducing heat production and up-lifting dietary macronutrient specifications are the two most studied dietary modifications. Replacing dietary CP with synthetic amino acids (lysine, tryptophan and threonine) can reduce heat production (Kerr et al., 2003), but the growth rate was not improved under hot conditions (Kerr et al., 2003; Spencer et al., 2005; Wolp et al., 2012). Simply reducing dietary CP did not change heat production in growing pigs, and it reduced growth and protein deposition rate (Kerr et al., 2003), thus it is not recommended. Increasing soybean oil inclusion rate from 1.5% to 4.5% in the isocaloric diets improved both feed efficiency (gain: feed) and growth rate by 8% in grower pigs under hot conditions (Wolp et al., 2012). Up-lifting dietary macronutrient specifications such as amino acids or energy can improve growth rate under hot conditions. For example, supplementing synthetic essential amino acids increased the amino acid intake and growth rate of growing pigs under hot conditions (Morales et al., 2018). Increasing fat inclusion rate from 1% to 8% while achieving a greater energy density (from 13.6 to 14.9 MJ metabolisable energy/kg; fixed lysine to metabolisable energy ratio) improved growth rate and feed efficiency by 8% and 15%, respectively, in grower pigs under hot conditions, but it tended to increase carcass backfat thickness by 5% at a fixed carcass weight (Spencer et al., 2005). Up-lifting dietary macronutrient specifications can markedly increase diet costs. For example, every MJ increase of digestible energy (at a fixed lysine to energy ratio) in wheat- and barley-based grower/finisher phase diet increases diet cost by 10–15% based on Australian grain prices. Therefore, the cost and benefit of such a summer feeding regime must be evaluated according to each feed-to-pork margin scenario.

Some growth-promoting micronutrients have been recently studied to mitigate HS impacts on growth performance due to their relatively low supplementation cost compared with macronutrients. Chromium has been a candidate which is known to improve insulin sensitivity (Matthews et al., 2001) and growth performance (Sales and Jancik, 2011). But recent Australian studies showed that chromium supplementation did not improve the growth rate under a cyclic HS condition (Liu et al., 2017) or summer conditions (Hung et al., 2014). An effective micro-nutrient supplement for improving growth rate and carcass weight of pigs under HS conditions is yet to be identified.

#### *Compromised intestinal barrier function due to acute heat stress*

During HS, pigs redistribute cardiac output away from splanchnic tissues to the skin and ears to enable heat dissipation (Collin et al., 2001), which may have negative effects on intestinal barrier function. Acute HS was reported can impair the intestinal barrier function in addition to its inhibitive effect on feed intake (Pearce et al., 2013b). These effects have been confirmed by a series of studies (Liu et al., 2016; Cottrell et al., 2020; Le et al., 2020). Oxidative stress is one of the possible modes of action. Specifically, a reduced glutathione peroxidase activity and reduced glutathione to oxidised glutathione ratio were found in the small intestine of pigs exposed to two days of cyclic HS (Liu et al., 2016). Studies reported inconsistent changes in inflammatory biomarkers in intestinal tissues in pigs subject to HS (Liu et al., 2016; Le et al., 2020). Circulating endotoxin increased by 50% in the pigs that

had increased intestinal permeability after exposure to short-term cyclic HS (including effects from the reduced feed intake) (Gabler et al., 2018). Thus, it is likely that the translocation of the pathogen can trigger systemic inflammation. In the muscle tissue, the inflammatory response seems time-dependent with the duration of thermal exposure. Increased inflammatory biomarkers were found in the oxidative type porcine muscle after 4, 6 and 12 hours of heat exposure (Ganesan et al., 2016; 2017), but such an effect was not seen after 72 hours of thermal exposure (Montilla et al., 2014). It is unknown whether the muscular inflammatory response is related to the increased endotoxin in pigs exposed to HS. The inflammatory response during short-term HS is likely to reduce the energy expenditure for growth performance. Cyclic HS conditions slightly reduced the standardised ileal digestibility of histidine (92.5–90%) and arginine (94–92%) (Morales et al., 2016) but did not affect fat digestibility (Kellner et al., 2016) in growing pigs. It remains unclear whether this magnitude of reduction in amino acid digestibility plays a role in the reduced growth rate.

#### *Solutions to mitigate heat stress impacts on intestinal barrier function*

Several micronutrients have been identified for alleviating the impacts of HS on intestinal barrier function and inflammatory response in grower pigs. Supra-nutritional level of yeast selenium (0.5 ppm) and vitamin E (100 IU/kg) successfully mitigated the acute HS impaired barrier function in grower pigs (Liu et al., 2016). Cinnamon supplementation improved intestinal barrier function in grower pigs under HS conditions (Cottrell et al., 2020). Betaine (1 g/kg) as well as isoquinoline alkaloids (150 mg/kg) supplemented diet improved colonic permeability in heat-stressed pigs (Le et al., 2020). A recent study showed that supplementing with recombinant superoxide dismutase (rSOD, 50 IU/day) or a combination of selenium (0.3 ppm) and rSOD (50 IU/day) ameliorated HS-induced inflammation as demonstrated by a lower concentration of circulating adiponectin, interleukin-1 $\beta$  and interleukin-6 (Le et al., 2019).

#### *Attenuated fat mobilisation and its potential effect on carcass composition*

As mentioned above, the Australian pig market penalises carcass fatness. However, carcass fatness during summer is not a current issue for such a market due to the overall low carcass weights usually seen during summer (Trezona et al., 2004). However, understanding the effects of HS on fat deposition in grower/finisher pigs will be of interest if pig producers plan to develop heavy carcass markets during the summer season in future. The effects of HS during the grower/finisher phase on carcass fatness were inconsistent (Table 2). When comparing heat-stressed pigs with the thermoneutral pigs fed *ad libitum*, most studies reported a reduced backfat thickness along with reduced feed intake, growth rate, and carcass weight (Le Bellego et al., 2002; Boddicker et al., 2014; Cruzen et al., 2015). By comparison, Ma et al., (2019) reported that 3 weeks of HS reduced feed intake by 50%, reduced final weight by 15%, but increased backfat by 26%. The reason for the increased backfat in the carcass with reduced weight is not known. When comparing heat-stressed pigs with pair-fed thermoneutral pigs, some studies found that HS increased flare fat percentage without affecting growth performance, carcass weight, or backfat (Christon, 1988; Kouba et al., 2001; Wu et al., 2016). More research should be conducted in future to examine the impacts of HS on carcass fatness in the finisher pigs slaughtered at fixed BW.

Mechanistically, there is some evidence that HS can attenuate fat mobilisation in growing pigs. Multiple studies have shown that pigs exposed to HS conditions for several days had a reduction in circulating non-esterified fatty acids (NEFAs), a marker of lipolysis



**Table 2**  
Effects of postnatal heat stress on carcass fatness of progeny pigs.

Studies	Thermal exposure	Feed intake	Growth rate	Gain: Feed	Carcass weight	Carcass fatness
Christon (1988)	22–32 °C finisher phase	↓17%	↓39%	↓30%	↓9%	Backfat thickness→ Backfat weight%→ Flare fat weight%↑27%
Le Bellego et al. (2002)	29 °C finisher phase	↓20%	↓16%	→	Fixed weight	Backfat thickness↓10% Fat composition↓8%
Boddicker et al. (2014)	35 °C finisher phase	↓30%	↓26%	→	↓9.5 kg	Backfat thickness↓20%
Cruzen et al. (2015)	32 °C finisher phase	↓21%	↓28%	→	↓5%	Backfat thickness↓16% Perirenal fat%→
Ma et al. (2019)	35 °C finisher phase	↓50%	↓62%	↓24%	↓15%	Backfat thickness↑26% Flare fat weight→
Serviento et al. (2020)	28–34 °C finisher phase	↓12%	↓11%	→	↓5%	Backfat thickness→ Backfat weight%→ Perirenal fat%→
Christon (1988)	22–32 °C finisher phase	Pair-fed	→	→	→	Backfat thickness→ Backfat weight%→ Flare fat weight%↑47%
Kouba et al. (2001)	31 °C grower phase	Pair-fed	→	→	→	Backfat weight→ Flare weight%↑130%
Wu et al. (2016)	30 °C finisher phase	Pair-fed	NA	NA	→	Backfat thickness→ Backfat weight%↑22% Flare fat weight%↑43%
Ma et al. (2019)	35 °C finisher phase	Pair-fed	→	→	→	Backfat thickness→ Flare fat weight→

Abbreviations: → = unchanged; ↑ = increased; ↓ = reduced; NA = data not available.

(Pearce et al., 2013a; Sanz Fernandez et al., 2015; Cottrell et al., 2020). It has been reported that HS can inhibit fatty acid oxidation in the skeletal muscle in growing pigs (Wu et al., 2016; Zhao et al., 2018). Insulin, a potent antilipolytic hormone, was thought to be a factor for the attenuated lipid mobilisation, but studies showed that basal insulin concentration was either not significantly affected or reduced in the heat-stressed pigs with a reduction in NEFA concentration (Sanz Fernandez et al., 2015; Gabler et al., 2018). Moreover, heat-stressed pigs had reduced insulin secretion in response to glucose tolerant tests (Liu et al., 2017; Cottrell et al., 2020). Therefore, the attenuated lipolysis in the pigs is not likely due to hyperinsulinemia. Unlike the reduction in fat mobilisation, heat-stressed pigs showed an increased preference for using amino acids as energy sources. Heat stress increased muscle proteolysis to produce amino acids for utilisation, as evidenced by a 16% increase in circulating Nt-methyl histidine (Pearce et al., 2013a) and increased muscular leucine oxidation by 35% (Fausnacht et al., 2021). The utilisation of muscle protein reflected increased gluconeogenesis to provide glucose as an energy source under HS conditions.

### Economic impacts of heat stress in the pig industry

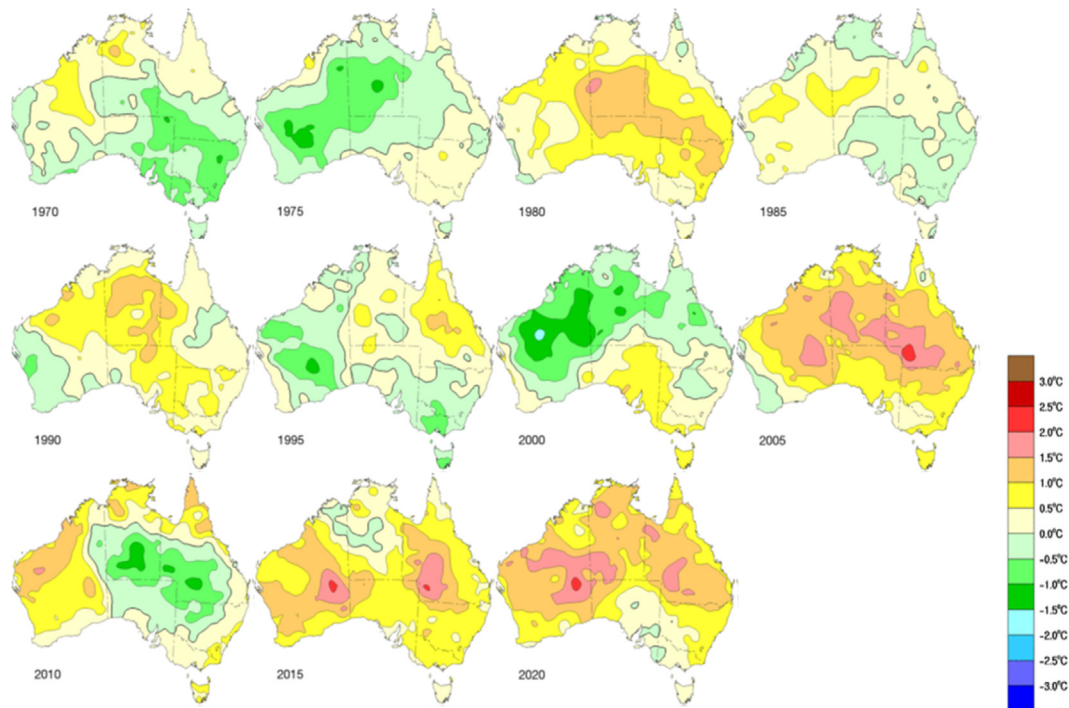
It is difficult to generalise the economic impacts of HS in the global pig industry. Some countries have estimated the economic impacts based on their climatic conditions. For example, it is estimated that the HS conditions in the USA prolong non-reproductive days of sows, reduce the growth rate of grower/finisher pigs, and increase mortality rate, resulting in an annual loss of USD 300 million in the pig industry (St-Pierre et al., 2003). The economic loss associated with the impacts of summer HS in the Australian pig industry has not been previously estimated. A simplified estimation is attempted here to quantify the economic loss due to the three major impacts discussed above. In 2019, there were 269 400 breeding sows in Australia with an annual slaughter number of 5.5 million (Australian Bureau of Statistics, 2020). The pig inventory data in 2019 were used for estimating the economic impacts of HS.

For the first impact, more sows are usually required to be mated for maintaining the supply of finisher pigs to the market when

sows that mated in summer have a lower farrowing rate. Assuming the average farrowing rate reduced from 89% to 75% (Liu et al., 2020), the piggery would need to increase the number of matings over summer by 18% to maintain the same number of piglets born. Assuming 14% of mated sows returned to oestrus after day 35, the increased cost of feeding 18% more sows and increased non-reproductive days (4 days on average for the sow herd) will incur a loss of farm profit by AUD 2.7 per finisher pig. For the 1.25 million finisher pigs (2019–2020 data from the Australian Bureau of Statistics (2020)) that were produced from the sows mated in summer in Australia, the economic loss, due to the increased cost of production, is equivalent to AUD 3.4 million.

For the second impact, on sows that manage to farrow after summer mating, an increased proportion (e.g.: from 15.8% to 24.2% (Liu et al., 2020)) of progeny are born with lightweight. The poorer growth rate and high adiposity of born-light progeny pigs can result in prolonged days to reach a marketable BW and higher carcass fatness of the progeny population (Liu et al., 2020). Liu et al., (2020) estimated that progeny born to summer mated sows had increased their average carcass backfat thickness by 0.33 mm at a carcass weight of 77 kg. If the average carcass backfat increased from 11.7 to 12.0 mm, then the penalty associated with the high backfat thickness (assuming a \$0.4/kg carcass weight penalty applies when backfat is >12 mm) would result in an average loss of carcass value of AUD 4.2 per progeny born to the sows mated in summer. This is equivalent to AUD 5.3 million for the 1.25 million finisher pigs that are produced from the sows mated in summer in Australia. The low survival rate and inferior growth rate of the born-light piglets can cause additional economic loss depending on the production system, which has not been included in this calculation.

For the third impact, the slowed growth rate of pigs during summer can reduce carcass weight and consequently limits the revenue of pig producers. For instance, if the summer condition reduces the feed intake and growth rate of finisher pigs by 8% (data referenced from Lewis and Bunter (2011)), the carcass weight can drop by approximately 5 kg due to slowed growth rate in this peak pork consumption season. The economic loss, due to the lighter carcass weight, is estimated to be AUD 10.9 for each carcass marketed during summer or equivalent to AUD 13.6 million for the 1.25 million finisher pigs slaughtered during summer. To sum up,



**Fig. 5.** Anomaly of mean climate temperature in Australia from 1970 to 2020. Map legend shows the anomaly of temperature compared to the average over the reference period of 1961–1990. Data were sourced from <http://www.bom.gov.au/climate/history/temperature>.

the economic loss due to the three major impacts of summer HS in the Australian pig industry is estimated to be AUD 22.3 million per year. The actual economic loss is likely to be much higher when the death of pigs resulting from extreme heat events, energy, and water usage for cooling, and labour cost, etc are taken into consideration. This simplified estimation may not accurately reflect the true economic losses, due to the varied magnitude of HS impacts among farms; however, each farm can calculate its financial loss by evaluating the three impacts from their production record.

### Global warming and future prospectus

Global warming manifests as a rise in the average environmental temperature and an increased frequency of extremely hot days. For example, the average Australian temperature has warmed by 1.4 °C in comparison to 1910 and by 1.0 °C in comparison to 1960 (when intensive pig farming started in Australia), respectively (Fig. 5). In 2019, 33 days exceeded 39 °C, which was more than the combined number (24 days) recorded between 1960 and 2018 (CSIRO and Australian Bureau of Meteorology, 2020). It is unknown whether natural selection occurred in the past decades, with respect to the resilience of pigs to HS, and whether this occurred at the pace of global warming, as few studies have quantified the progressive impacts of global warming on pig productivity. Australia's climate model has predicted that the average Australian temperature will become 2.0 °C warmer than the pre-industrial period (1810–1900) by 2040, with the ongoing emission of greenhouse gases (CSIRO and Australian Bureau of Meteorology, 2020). We assume that the trend of global warming will worsen the impacts associated with summer conditions on pig productivity, due to the positive correlation between the environmental temperature and the physiological impacts on pigs.

Improving the efficiency of pig production under summer conditions is an important goal for sustaining food production under challenging climate conditions. Progress in understanding the physiological impacts of HS will aid in this goal and will assist in the development of management strategies to improve the resili-

ence of pigs under these challenging conditions. The current needs of the pig industry are commercially viable solutions to (1) reduce early pregnancy loss of sows mated in summer, (2) to improve foetal development of the progeny pigs born to the sows mated and gestated in summer, and (3) to develop strategies to improve the growth rate of finisher pigs under hot conditions. The majority of the solutions investigated in the past decade are mainly nutrition-based. In future, strategies such as implementing cost-effective cooling strategies, breeding genetics with better heat resilience, etc. should also be explored. Of course, all of the above should be coupled with strategies to reverse the pace of global warming itself.

### Conclusion

The HS conditions in summer reduce pig production efficiency. Reduced farrowing rate of sows mated in summer, increased carcass fatness of pigs born to the sows mated in summer, and reduced growth rate and carcass weights of pigs finished under hot conditions are the three major impacts causing a significant economic loss in the pig industry. The worldwide research conducted in the past decade has progressed our understanding on the physiological mechanism behind these impacts. Some mitigation strategies have exhibited beneficial effects on the impacts, but the pig industry still requires a broad range of commercially viable strategies to tackle those issues. To combat the negative impacts of summer conditions, three specific research directions should be continued (1) to reduce early pregnancy loss of sows mated in summer, (2) to understand the impacts of gestational HS in foetal development and develop mitigation strategies that reduce carcass fatness of progeny pigs born to the sows mated in summer, and (3) to develop strategies to improve feed intake and growth rate of finisher pigs under hot conditions.

### Ethics approval

Not applicable

**Data and model availability statement**

Not applicable.

**Author ORCIDs**

**F. Liu:** <https://orcid.org/0000-0003-2644-2416>  
**W. Zhao:** <https://orcid.org/0000-0002-3055-6275>  
**H.H. Le:** <https://orcid.org/0000-0001-8649-6892>  
**J.J. Cottrell:** <https://orcid.org/0000-0002-1899-2090>  
**M.P. Green:** <https://orcid.org/0000-0002-6076-9781>  
**B.J. Leury:** <https://orcid.org/0000-0001-9173-2730>  
**F.R. Dunshea:** <https://orcid.org/0000-0003-3998-1240>

**Author contributions**

**Fan Liu:** Writing- Original Draft, Writing- Review & Editing, Visualisation

**Weicheng Zhao:** Writing- Original Draft, Writing- Review & Editing

**Hieu L. Le:** Writing- Original Draft

**Jeremy J. Cottrell:** Writing- Review & Editing

**Mark P. Green:** Writing- Review & Editing

**Brian J. Leury:** Writing- Review & Editing

**Frank R. Dunshea:** Writing- Review & Editing

**Alan W. Bell:** Writing- Review & Editing

**Declaration of interest**

None.

**Acknowledgements**

None.

**Financial support statement**

None.

**References**

- Alvarenga Dias, A.L., Chiarini-Garcia, H., Cardeal, P.C., Moreira, L., Foxcroft, G., Fontes, D., Almeida, F., 2012. Intra-uterine growth retardation affects birthweight and postnatal development in pigs, impairing muscle accretion, duodenal mucosa morphology and carcass traits. *Reproduction, Fertility, and Development* 25, 387–395.
- Alvarez Sedó, C., Bilinski, M., Lorenzi, D., Uriondo, H., Noblíá, F., Longobucco, V., Lagar, E.V., Nodar, F., 2017. Effect of sperm DNA fragmentation on embryo development: clinical and biological aspects. *JBRA Assisted Reproduction* 21, 343–350.
- Australian Bureau of Statistics, 2020. *Livestock and Meat, Australia*. Retrieved on 7 April 2020, from <https://www.abs.gov.au/statistics/industry/agriculture/livestock-and-meat-australia/latest-release>.
- Bell, A., Wilkening, R., Meschia, G., 1987. Some aspects of placental function in chronically heat-stressed ewes. *Journal of Developmental Physiology* 9, 17–29.
- Bernhard, C.J., Sharp, K.G., Safranski, T.J., Lamberson, W.R., Lucy, M.C., 2020. Reproduction and reproductive tract morphology of male and female pigs whose mothers were heat stressed during the second month of gestation. *Journal of Animal Science* 2020. <https://doi.org/10.1093/jas/skaa352>. Published online by Oxford University Press 28 October.
- Bertoldo, M., Holyoake, P.K., Evans, G., Grupen, C.G., 2010. Oocyte developmental competence is reduced in sows during the seasonal infertility period. *Reproduction Fertility and Development* 22, 1222–1229.
- Bertoldo, M., Holyoake, P.K., Evans, G., Grupen, C.G., 2011. Follicular progesterone levels decrease during the period of seasonal infertility in sows. *Reproduction in Domestic Animals* 46, 489–494.
- Bertoldo, M.J., Nadal-Desbarats, L., Gerard, N., Dubois, A., Holyoake, P.K., Grupen, C.G., 2013. Differences in the metabolomic signatures of porcine follicular fluid collected from environments associated with good and poor oocyte quality. *Reproduction* 146, 221–231.
- Bidne, K.L., Romoser, M.R., Ross, J.W., Baumgard, L.H., Keating, A.F., 2019. Heat stress during the luteal phase decreases luteal size but does not affect circulating progesterone in gilts. *Journal of Animal Science* 97, 4314–4322.
- Boddicker, R.L., Seibert, J.T., Johnson, J.S., Pearce, S.C., Selsby, J.T., Gabler, N.K., Lucy, M.C., Safranski, T.J., Rhoads, R.P., Baumgard, L.H., Ross, J.W., 2014. Gestational heat stress alters postnatal offspring body composition indices and metabolic parameters in pigs. *PLoS ONE* 9, e110859.
- Bunz, A., Bunter, K., Morrison, R., Luxford, B., Hermes, S., 2019. Differences in farrowing rate according to parity and trait specific temperature groupings around mating events. In: *Proceedings of the 17th Biennial Conference of the Australasian Pig Science Association*, 17–20 November 2019, Adelaide, Australia, p. s09.
- Cabezón, F.A., Stewart, K.R., Schinckel, A.P., Richert, B.T., 2017. Effects of betaine and heat stress on lactation and postweaning reproductive performance of sows. *The Professional Animal Scientist* 33, 241–253.
- Chang, E.I., Rozance, P.J., Wesolowski, S.R., Nguyen, L.M., Shaw, S.C., Sclafani, R.A., Bjorkman, K.K., Peter, A.K., Hay, W.W., Brown, L.D., 2020. Rates of myogenesis and myofiber numbers are reduced in late gestation IUGR fetal sheep. *Journal of Endocrinology* 244, 339–352.
- Choi, J., Kwon, K., Lee, Y., Ko, E., Kim, Y., Choi, Y., 2019. Characteristics of pig carcass and primal cuts measured by the autofluorescence depend on seasonal classification. *Food Science of Animal Resources* 39, 332–344.
- Christon, R., 1988. The effect of tropical ambient temperature on growth and metabolism in pigs. *Journal of Animal Science* 66, 3112–3123.
- Collin, A., Lebreton, Y., Fillaut, M., Vincent, A., Thomas, F., Herpin, P., 2001. Effects of exposure to high temperature and feeding level on regional blood flow and oxidative capacity of tissues in piglets. *Experimental Physiology* 86, 83–91.
- Cottrell, J.J., Furness, J.B., Wijesiriwardana, U.A., Ringuet, M., Liu, F., DiGiacomo, K., Leury, B.J., Clarke, J.L., Dunshea, F.R., 2020. The effect of heat stress on respiratory alkalosis and insulin sensitivity in cinnamon supplemented pigs. *Animals* 10, 690.
- Cruzen, S.M., Boddicker, R.L., Graves, K.L., Johnson, T.P., Arkfeld, E.K., Baumgard, L.H., Ross, J.W., Safranski, T.J., Lucy, M.C., Lonergan, S.M., 2015. Carcass composition of market weight pigs subjected to heat stress in utero and during finishing. *Journal of Animal Science* 93, 2587–2596.
- CSIRO and Australian Bureau of Meteorology, 2020. *State of the climate 2020*. Retrieved on 20 May, from <https://www.csiro.au/en/research/environmental-impacts/climate-change/state-of-the-climate>.
- da Fonseca de Oliveira, A.C., Vanelli, K., Sotomaior, C.S., Weber, S.H., Costa, L.B., 2019. Impacts on performance of growing-finishing pigs under heat stress conditions: a meta-analysis. *Veterinary Research Communications* 43, 37–43.
- Department of Primary Industries, 2016. *Pig breeds in Australia*. Retrieved on 7 April 2021, from [https://www.dpi.nsw.gov.au/\\_data/assets/pdf\\_file/0007/872683/Pig-breeds-brochure.pdf](https://www.dpi.nsw.gov.au/_data/assets/pdf_file/0007/872683/Pig-breeds-brochure.pdf).
- Edgerly, L.A., Kaminski, M.A., Silvia, W.J., 2000. Effects of progesterone and estradiol on uterine secretion of prostaglandin F<sub>2α</sub> in response to oxytocin in ovariectomized sows. *Biology of Reproduction* 62, 365–369.
- Fausnacht, D.W., Kroscher, K.A., McMillan, R.P., Martello, L.S., Baumgard, L.H., Selsby, J.T., Hulver, M.W., Rhoads, R.P., 2021. Heat stress reduces metabolic rate while increasing respiratory exchange ratio in growing pigs. *Animals* 11, 215.
- Fowden, A.L., Forhead, A.J., 2009. Hormones as epigenetic signals in developmental programming. *Experimental Physiology* 94, 607–625.
- Gabler, N.K., Koltz, D., Schaumberger, S., Murugesan, G.R., Reisinger, N., 2018. Diurnal heat stress reduces pig intestinal integrity and increases endotoxin translocation. *Translational Animal Science* 2, 1–10.
- Ganesan, S., Reynolds, C., Hollinger, K., Pearce, S.C., Gabler, N.K., Baumgard, L.H., Rhoads, R.P., Selsby, J.T., 2016. Twelve hours of heat stress induces inflammatory signaling in porcine skeletal muscle. *American Journal of Physiology - Regulatory, Integrative and Comparative Physiology* 310, R1288–R1296.
- Ganesan, S., Volodina, O., Pearce, S.C., Gabler, N.K., Baumgard, L.H., Rhoads, R.P., Selsby, J.T., 2017. Acute heat stress activated inflammatory signaling in porcine oxidative skeletal muscle. *Physiological Reports* 5, e13397.
- Geisert, R.D., Brookbank, J.W., Roberts, R.M., Bazer, F.W., 1982. Establishment of pregnancy in the pig: II. Cellular remodeling of the porcine blastocyst during elongation on day 12 of pregnancy. *Biology of Reproduction* 27, 941–955.
- Geisert, R.D., Zavy, M.T., Moffatt, R.J., Blair, R.M., Yellin, T., 1990. Embryonic steroids and the establishment of pregnancy in pigs. *Journal of Reproduction and Fertility Supplement* 40, 293–305.
- Giudice, L.C., 1992. Insulin-like growth factors and ovarian follicular development. *Endocrine Reviews* 13, 641–669.
- Hammer, M.A., Baltz, J.M., 2002. Betaine is a highly effective organic osmolyte but does not appear to be transported by established organic osmolyte transporters in mouse embryos. *Molecular Reproduction and Development* 62, 195–202.
- Hermesch, S., Bunz, A., 2020. 2017–2208 Genetic variation in seasonal infertility. *Australian Pork Limited, Barton, Australia*.
- Huang, S.Y., Kuo, Y.H., Lee, Y.P., Tsou, H.L., Lin, E.C., Ju, C.C., Lee, W.C., 2000. Association of heat shock protein 70 with semen quality in boars. *Animal Reproduction Science* 63, 231–240.
- Hung, A.T., Leury, B.J., Sabin, M.A., Collins, C.L., Dunshea, F.R., 2014. Dietary nano-chromium tripicolinate increases feed intake and decreases plasma cortisol in finisher gilts during summer. *Tropical Animal Health and Production* 46, 1483–1489.
- Hunter, M., 2000. Oocyte maturation and ovum quality in pigs. *Reviews of Reproduction* 5, 122–130.

- Huynh, T.T.T., Aarnink, A.J.A., Verstegen, M.W.A., Gerrits, W.J.J., Heetkamp, M.J.W., Kemp, B., Canh, T.T., 2005. Effects of increasing temperatures on physiological changes in pigs at different relative humidities. *Journal of Animal Science* 83, 1385–1396.
- Johnson, J.S., Sanz Fernandez, M.V., Gutierrez, N.A., Patience, J.F., Ross, J.W., Gabler, N.K., Lucy, M.C., Safranski, T.J., Rhoads, R.P., Baumgard, L.H., 2015a. Effects of in utero heat stress on postnatal body composition in pigs: I. Growing phase. *Journal of Animal Science* 93, 71–81.
- Johnson, J.S., Sanz Fernandez, M.V., Patience, J.F., Ross, J.W., Gabler, N.K., Lucy, M.C., Safranski, T.J., Rhoads, R.P., Baumgard, L.H., 2015b. Effects of in utero heat stress on postnatal body composition in pigs: II. Finishing phase. *Journal of Animal Science* 93, 82–92.
- Kellner, T.A., Baumgard, L.H., Prusa, K.J., Gabler, N.K., Patience, J.F., 2016. Does heat stress alter the pig's response to dietary fat? *Journal of Animal Science* 94, 4688–4703.
- Kemp, B., Soede, N.M., 1996. Relationship of weaning-to-estrus interval to timing of ovulation and fertilization in sows. *Journal of Animal Science* 74, 944–949.
- Kerr, B.J., Yen, J.T., Nienaber, J.A., Easter, R.A., 2003. Influences of dietary protein level, amino acid supplementation and environmental temperature on performance, body composition, organ weights and total heat production of growing pigs. *Journal of Animal Science* 81, 1998–2007.
- Khan, A., Dou, J., Wang, Y., Jiang, X., Khan, M.Z., Luo, H., Usman, T., Zhu, H., 2020. Evaluation of heat stress effects on cellular and transcriptional adaptation of bovine granulosa cells. *Journal of Animal Science and Biotechnology* 11, 25.
- King, R.H., 2017. Seasonal infertility in pigs: what have we achieved and where are we up to? *Animal Production Science* 57, 2325–2330.
- Kouba, M., Hermier, D., Le Dividich, J., 2001. Influence of a high ambient temperature on lipid metabolism in the growing pig. *Journal of Animal Science* 79, 81–87.
- Krisner, R.L., 2004. The effect of oocyte quality on development. *Journal of Animal Science* 82, E14–E23.
- Le Bellego, L., van Milgen, J., Noblet, J., 2002. Effect of high temperature and low-protein diets on the performance of growing-finishing pigs. *Journal of Animal Science* 80, 691–701.
- Le, H.H., Shakeri, M., Suleria, H.A.R., Zhao, W., McQuade, R.M., Phillips, D.J., Vidacs, E., Furness, J.B., Dunshea, F.R., Artuso-Ponte, V., Cottrell, J.J., 2020. Betaine and isoquinoline alkaloids protect against heat stress and colonic permeability in growing pigs. *Antioxidants* 9, 1024.
- Le, H.H., Vidacs, E., Phillips, D.J., Zhao, W., Furness, J.B., Gabler, N.K., Renaudeau, D., Wijffels, G., Dunshea, F.R., DiGiacomo, K., Roura, E., Leury, B.J., Cottrell, J.J., 2019. Effect of selenium and superoxide dismutase supplementation on heat stressed pigs. *Journal of Animal Science* 97 (suppl. 2), 179.
- Lewis, C., Bunter, K., 2011. Effects of seasonality and ambient temperature on genetic parameters for production and reproductive traits in pigs. *Animal Production Science* 51, 615–626.
- Limesand, S., Camacho, L., Kelly, A., Antolic, A., 2018. Impact of thermal stress on placental function and fetal physiology. *Animal Reproduction* 15, 886–898.
- Lin, Y., Lv, G., Dong, H., Wu, D., Tao, Z., Xu, S., Che, L., Fang, Z., Bai, S., Feng, B., Li, J., Xu, X., 2017. Effects of the different levels of dietary vitamin D on boar performance and semen quality. *Livestock Science* 203, 63–68.
- Liu, F., Braden, C.J., Smits, R.J., Craig, J.R., Henman, D.J., Brewster, C.J., Morrison, R.S., Athorn, R.Z., Leury, B.J., Zhao, W., Cottrell, J.J., Dunshea, F.R., Bell, A.W., 2021b. Compensatory feeding during early gestation for sows with a high weight loss after a summer lactation increased piglet birth weight but reduced litter size. *Journal of Animal Science* 99, skab228.
- Liu, F., Brewster, C., Henman, D., Smits, R., Craig, J., 2021a. 2018–0023 Optimise the duration of betaine supplementation in pig production. Australian Pork Limited, Barton, Australia.
- Liu, F., Cottrell, J.J., Furness, J.B., Rivera, L.M., Kelly, F.W., Wijesiriwardana, U., Pustovit, R.V., Fothergill, L.J., Bravo, D.M., Celi, P., Leury, B.J., Gabler, N.K., Dunshea, F.R., 2016. Selenium and vitamin E together improve intestinal epithelial barrier function and alleviate oxidative stress in heat-stressed pigs. *Experimental Physiology* 101, 801–810.
- Liu, F., Cottrell, J.J., Wijesiriwardana, U., Kelly, F.W., Chauhan, S.S., Pustovit, R.V., Gonzales-Rivas, P.A., DiGiacomo, K., Leury, B.J., Celi, P., Dunshea, F.R., 2017. Effects of chromium supplementation on physiology, feed intake, and insulin related metabolism in growing pigs subjected to heat stress. *Translational Animal Science* 1, 116–125.
- Liu, F., de Ruyter, E.M., Athorn, R.Z., Brewster, C.J., Henman, D.J., Morrison, R.S., Smits, R.J., Cottrell, J.J., Dunshea, F.R., 2019. Effects of L-citrulline supplementation on heat stress physiology, lactation performance and subsequent reproductive performance of sows in summer. *Journal of Animal Physiology and Animal Nutrition* 103, 251–257.
- Liu, F., Ford, E.M., Morrison, R.S., Brewster, C.J., Henman, D.J., Smits, R.J., Zhao, W., Cottrell, J.J., Leury, B.J., Dunshea, F.R., Bell, A.W., 2020. The greater proportion of born-light progeny from sows mated in summer contributes to increased carcass fatness observed in spring. *Animals* 10, 2080.
- Love, R.J., Evans, G., Klupiec, C., 1993. Seasonal effects on fertility in gilts and sows. *Journal of Reproduction and Fertility Supplement* 48, 191–206.
- Lucy, M., Safranski, T., Rhoads, J., Ross, J., Gabler, N., Rhoads, R., Baumgard, L., 2012. Litter characteristics and thermoregulatory behavior of first parity sows exposed to a controlled heat stress (HS) during gestation. *Journal of Animal Science* 90 (suppl. 3), 731–732.
- Lugar, D.W., Harlow, K.E., Hundley, J., Goncalves, M., Bergstrom, J., Stewart, K.R., 2019. Effects of increased levels of supplemental vitamins during the summer in a commercial artificial insemination boar stud. *Animal* 13, 2556–2568.
- Ma, X., Wang, L., Shi, Z., Chen, W., Yang, X., Hu, Y., Zheng, C., Jiang, Z., 2019. Mechanism of continuous high temperature affecting growth performance, meat quality, and muscle biochemical properties of finishing pigs. *Genes & Nutrition* 14, 23.
- Matthews, J.O., Southern, L.L., Fernandez, J.M., Pontif, J.E., Bidner, T.D., Odgaard, R.L., 2001. Effect of chromium picolinate and chromium propionate on glucose and insulin kinetics of growing barrows and on growth and carcass traits of growing-finishing barrows. *Journal of Animal Science* 79, 2172–2178.
- Meyer, A.E., Pfeiffer, C.A., Brooks, K.E., Spate, L.D., Benne, J.A., Cecil, R., Samuel, M.S., Murphy, C.N., Behura, S., McLean, M.K., Ciernia, L.A., Smith, M.F., Whitworth, K.M., Wells, K.D., Spencer, T.E., Prather, R.S., Geisert, R.D., 2019. New perspective on conceptus estrogens in maternal recognition and pregnancy establishment in the pig. *Biology of Reproduction* 101, 148–161.
- Montilla, S.I.R., Johnson, T.P., Pearce, S.C., Gardan-Salmon, D., Gabler, N.K., Ross, J.W., Rhoads, R.P., Baumgard, L.H., Lonergan, S.M., Selsby, J.T., 2014. Heat stress causes oxidative stress but not inflammatory signaling in porcine skeletal muscle. *Temperature* 1, 13–21.
- Morales, A., Chávez, M., Vásquez, N., Htoo, J.K., Buenabad, L., Espinoza, S., Cervantes, M., 2018. Increased dietary protein or free amino acids supply for heat stress pigs: effect on performance and carcass traits. *Journal of Animal Science* 96, 1419–1429.
- Morales, A., Pérez, M., Castro, P., Ibarra, N., Bernal Barragan, H., Baumgard, L., Cervantes, M., 2016. Heat stress affects the apparent and standardized ileal digestibilities of amino acids in growing pigs. *Journal of Animal Science* 94, 3362–3369.
- Parrish, J.J., Willenburg, K.L., Gibbs, K.M., Yagoda, K.B., Krautkramer, M.M., Loether, T.M., Melo, F.C.S.A., 2017. Scrotal insulation and sperm production in the boar. *Molecular Reproduction and Development* 84, 969–978.
- Pearce, S.C., Gabler, N.K., Ross, J.W., Escobar, J., Patience, J.F., Rhoads, R.P., Baumgard, L.H., 2013a. The effects of heat stress and plane of nutrition on metabolism in growing pigs. *Journal of Animal Science* 91, 2108–2118.
- Pearce, S.C., Mani, V., Weber, T.E., Rhoads, R.P., Patience, J.F., Baumgard, L.H., Gabler, N.K., 2013b. Heat stress and reduced plane of nutrition decreases intestinal integrity and function in pigs. *Journal of Animal Science* 91, 5183–5193.
- Peltoniemi, O.A.T., Love, R.J., Heinonen, M., Tuovinen, V., Saloniemi, H., 1999. Seasonal and management effects on fertility of the sow: a descriptive study. *Animal Reproduction Science* 55, 47–61.
- Peña Jr., S.T., Stone, F., Gummow, B., Parker, A.J., Paris, D.B.B.P., 2019a. Tropical summer induces DNA fragmentation in boar spermatozoa: implications for evaluating seasonal infertility. *Reproduction, Fertility and Development* 31, 590–601.
- Peña Jr., S.T., Gummow, B., Parker, A.J., Paris, D.B.B.P., 2019b. Antioxidant supplementation mitigates DNA damage in boar (*Sus scrofa domestica*) spermatozoa induced by tropical summer. *PLoS ONE* 14, e0216143.
- Plush, K., Glencorse, D., Alexopoulos, J., Tritton, S., Kirkwood, R., D'Souza, D., 2019. Effect of dextrose supplementation in the pre-ovulatory sow diet to reduce seasonal influences on litter birth weight variation. *Animals* 9, 1009.
- Putney, D.J., Malayer, J.R., Gross, T.S., Thatcher, W.W., Hansen, P.J., Drost, M., 1988. Heat stress-induced alterations in the synthesis and secretion of proteins and prostaglandins by cultured bovine conceptuses and uterine endometrium. *Biology of Reproduction* 39, 717–728.
- Quiniou, N., Noblet, J., 1999. Influence of high ambient temperatures on performance of multiparous lactating sows. *Journal of Animal Science* 77, 2124–2134.
- Renaudeau, D., Gourdière, J.L., St-Pierre, N.R., 2011. A meta-analysis of the effects of high ambient temperature on growth performance of growing-finishing pigs. *Journal of Animal Science* 89, 2220–2230.
- Robinson, L., Gallos, I.D., Conner, S.J., Rajkhowa, M., Miller, D., Lewis, S., Kirkman-Brown, J., Coomarasamy, A., 2012. The effect of sperm DNA fragmentation on miscarriage rates: a systematic review and meta-analysis. *Human Reproduction* 27, 2908–2917.
- Rodríguez-Sánchez, J.A., Ripoll, G., Calvo, S., Ariño, L., Latorre, M.A., 2009. The effect of seasonality of the growing-finishing period on carcass, meat and fat characteristics of heavy barrows and gilts. *Meat Science* 83, 571–576.
- Rosero, D.S., Boyd, R.D., McCulley, M., Odle, J., van Heugten, E., 2016. Essential fatty acid supplementation during lactation is required to maximize the subsequent reproductive performance of the modern sow. *Animal Reproduction Science* 168, 151–163.
- Rozance, P.J., Zastoupil, L., Wesolowski, S.R., Goldstrohm, D.A., Strahan, B., Cree-Green, M., Sheffield-Moore, M., Meschia, G., Hay Jr., W.W., Wilkening, R.B., Brown, L.D., 2018. Skeletal muscle protein accretion rates and hindlimb growth are reduced in late gestation intrauterine growth-restricted fetal sheep. *The Journal of Physiology* 596, 67–82.
- Sales, J., Jancik, F., 2011. Effects of dietary chromium supplementation on performance, carcass characteristics, and meat quality of growing-finishing swine: A meta-analysis. *Journal of Animal Science* 89, 4054–4067.
- Sanz Fernandez, M.V., Stoakes, S.K., Abuajamieh, M., Seibert, J.T., Johnson, J.S., Horst, E.A., Rhoads, R.P., Baumgard, L.H., 2015. Heat stress increases insulin sensitivity in pigs. *Physiological Reports* 3, e12478.
- Serviento, A.M., Lebret, B., Renaudeau, D., 2020. Chronic prenatal heat stress alters growth, carcass composition, and physiological response of growing pigs subjected to postnatal heat stress. *Journal of Animal Science* 2020. <https://doi.org/10.1093/jas/skaa161>. Published online by Oxford University Press 16 May.
- Setchell, B.P., 1998. The Parkes Lecture Heat and the testis. *Reproduction* 114, 179–194.

- Seyfang, J., Langendijk, P., Chen, T.Y., Bouwman, E., Kirkwood, R.N., 2016. Human chorionic gonadotrophin in early gestation induces growth of estrogenic ovarian follicles and improves primiparous sow fertility during summer. *Animal Reproduction Science* 172, 21–25.
- Smith, S., Liu, F., Tucker, B.S., Craig, J.R., Braden, C., Hourigan, D., Webb, M., Morrison, R.S., 2021. Lowering group size in electronic sow feeder gestation pens reduced skin injuries and improved reproductive outcomes of sows mated in summer. In: *Proceedings of the 18th Biennial Conference of the Australasian Pig Science Association*, 15–18 November 2021, Brisbane, Australia, p. s08.
- Spencer, J.D., Gaines, A.M., Berg, E.P., Allee, G.L., 2005. Diet modifications to improve finishing pig growth performance and pork quality attributes during periods of heat stress. *Journal of Animal Science* 83, 243–254.
- Spencer, T.E., Bazer, F.W., 2004. Conceptus signals for establishment and maintenance of pregnancy. *Reproductive Biology and Endocrinology* 2.
- St-Pierre, N.R., Cobanov, B., Schnitkey, G., 2003. Economic losses from heat stress by US livestock industries. *Journal of Dairy Science* 86, E52–E77.
- Stone, B.A., 1982. Heat induced infertility of boars: The inter-relationship between depressed sperm output and fertility and an estimation of the critical air temperature above which sperm output is impaired. *Animal Reproduction Science* 4, 283–299.
- Tamura, H., Takasaki, A., Miwa, I., Taniguchi, K., Maekawa, R., Asada, H., Taketani, T., Matsuoka, A., Yamagata, Y., Shimamura, K., Morioka, H., Ishikawa, H., Reiter, R.J., Sugino, N., 2008. Oxidative stress impairs oocyte quality and melatonin protects oocytes from free radical damage and improves fertilization rate. *Journal of Pineal Research* 44, 280–287.
- Tast, A., Peltoniemi, O.A., Virolainen, J.V., Love, R.J., 2002. Early disruption of pregnancy as a manifestation of seasonal infertility in pigs. *Animal Reproduction Science* 74, 75–86.
- Trezona, M., Mullan, B.P., D'Antuono, M., Wilson, R.H., Williams, I.H., 2004. The causes of seasonal variation in backfat thickness of pigs in Western Australia. *Australian Journal of Agricultural Research* 55, 273–277.
- Tuell, J.R., Nondorf, M.J., Maskal, J.M., Johnson, J.S., Kim, Y.H.B., 2021. Impacts of in utero heat stress on carcass and meat quality traits of market weight gilts. *Animals* 11, 717.
- Vallet, J.L., Christenson, R.K., Trout, W.E., Klemcke, H.G., 1998. Conceptus, progesterone, and breed effects on uterine protein secretion in swine. *Journal of Animal Science* 76, 2657–2670.
- van Wettere, W., 2013. Determining the effects of season on timing of ovulation and luteal function. Co-operative Research Centre for High Integrity Australian Pork, Willaston, Australia.
- van Wettere, W., Smits, R.J., Hughes, P.E., 2013. Methyl donor supplementation of gestating sow diets improves pregnancy outcomes and litter size. *Animal Production Science* 53, 1–7.
- Vatnick, I., Ignatz, G., McBride, B.W., Bell, A.W., 1991. Effect of heat stress on ovine placental growth in early pregnancy. *Journal of Developmental Physiology* 16, 163–166.
- Wathes, D.C., Abayasekara, D.R.E., Aitken, R.J., 2007. Polyunsaturated fatty acids in male and female reproduction. *Biology of Reproduction* 77, 190–201.
- Wettemann, R., Wells, M., Omtvedt, I., Pope, E., Turman, E., 1976. Influence of elevated ambient temperature on reproductive performance of boars. *Journal of Animal Science* 42, 664–669.
- Wolp, R.C., Rodrigues, N.E.B., Zangeronimo, M.G., Cantarelli, V.S., Fialho, E.T., Philomeno, R., Alvarenga, R.R., Rocha, L.F., 2012. Soybean oil and crude protein levels for growing pigs kept under heat stress conditions. *Livestock Science* 147, 148–153.
- Wu, X., Li, Z., Jia, A., Su, H., Hu, C., Zhang, M., Feng, J., 2016. Effects of high ambient temperature on lipid metabolism in finishing pigs. *Journal of Integrative Agriculture* 15, 391–396.
- Yates, D.T., Clarke, D.S., Macko, A.R., Anderson, M.J., Shelton, L.A., Nearing, M., Allen, R.E., Rhoads, R.P., Limesand, S.W., 2014. Myoblasts from intrauterine growth-restricted sheep fetuses exhibit intrinsic deficiencies in proliferation that contribute to smaller semitendinosus myofibres. *The Journal of Physiology* 592, 3113–3125.
- Zasiadczyk, L., Fraser, L., Kordan, W., Wasilewska, K., 2015. Individual and seasonal variations in the quality of fractionated boar ejaculates. *Theriogenology* 83, 1287–1303.
- Zhao, L., McMillan, R.P., Xie, G., Giridhar, S., Baumgard, L.H., El-Kadi, S., Selsby, J., Ross, J., Gabler, N., Hulver, M.W., Rhoads, R.P., 2018. Heat stress decreases metabolic flexibility in skeletal muscle of growing pigs. *American Journal of Physiology. Regulatory, Integrative and Comparative Physiology* 315, R1096–R1106.
- Zhao, W., Liu, F., Bell, A.W., Le, H.H., Cottrell, J.J., Leury, B.J., Green, M.P., Dunshea, F. R., 2020. Controlled elevated temperatures during early-mid gestation cause placental insufficiency and implications for fetal growth in pregnant pigs. *Scientific Reports* 10, 20677.