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Animal board invited review: Factors affecting the early growth and development of gilt progeny compared to sow progeny

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ABSTRACT

Progeny born to primiparous sows farrowing their first litter, often called gilt progeny (**GP**), are typically characterised by their poorer overall production performance than progeny from multiparous sows (sow progeny; **SP**). Gilt progeny consistently grow slower, are born and weaned lighter, and have higher post-weaning illness and mortality rates than SP. Collectively, their poorer performance culminates in a long time to reach market weight and, ultimately, reduced revenue. Due to the high replacement rates of sows, the primiparous sow and her progeny represent a large proportion of the herd resulting in a significant loss for the pig industry. While the reasons for poorer performance are complex and multifaceted, they may largely be attributed to the immature age at which gilts are often mated and the significant impact of this on their metabolism during gestation and lactation. As a result, this can have negative consequences on the piglet itself. To improve GP performance, it is crucial to understand the biological basis for differences between GP and SP. The purpose of this review is to summarise published literature investigating differences in growth performance and health status between GP and SP. It also examines the primiparous sow during gestation and lactation and how the young sow must support her own growth while supporting the metabolic demands of her pregnancy and the growth and development of her litter. Finally, the underlying physiology of GP is discussed in terms of growth and development in utero, the neonatal period, and the early development of the gastrointestinal tract. The present review concludes that there are a number of interplaying factors relating to the anatomy and physiology of the primiparous sow and of GP themselves. The studies presented herein strongly suggest that poor support of piglet growth in utero and reduced colostrum and milk production and consumption are largely responsible for the underperformance of GP. It is therefore recommended that future management strategies focus on supporting the primiparous sow during gestation and lactation, increasing the preweaning growth of GP to improve their ability to cope with the stressors of weaning, selection of reproductive traits such as uterine capacity to improve birth weights and ultimately GP performance, and finally, increase the longevity of sows to reduce the proportion of GP entering the herd.

Implications

Primiparous sows (gilts) are a vital component of pork production, making up a substantial proportion of the breeding herd. Therefore, the growth performance and health of gilt progeny are of the utmost importance, as they represent a significant proportion of total revenue. However, gilt progeny are often characterised by their compromised growth and development in comparison to progeny from multiparous sows. Focusing on supporting the physiological demands of gestation and lactation for the primiparous sow and improving the preweaning growth and development of gilt progeny will potentially improve their lifetime productivity.

Introduction

Progeny born to first litter (primiparous) sows, referred to as gilt progeny (**GP**), are generally perceived by pork producers as having poorer performance and a higher risk of mortality in comparison to sow progeny (**SP**). Due to their older age and prior experience as mothers, multiparous sows are regarded as being more

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physiologically, behaviourally, and immunologically mature than their primiparous counterparts. Consequently, SP are considered more robust and better able to deal with health challenges, grow faster, and have higher overall productivity than GP. Gilt progeny consistently grow slower, are born and weaned lighter (Miller et al., 2012a, Carney-Hinkle et al., 2013, Craig et al., 2017a), and have higher rates of postweaning illness and mortality compared to SP (Craig et al., 2017a). Collectively, the poorer production performance of GP results in a longer period taken to achieve optimal market weight and, ultimately, reduced revenue.

The replacement of breeder sows that either die or are removed from the breeding herd is essential to increase genetic gain and overall productivity. Global sow replacement rates have therefore remained high (Špinka and Illmann, 2015) being reported at approximately 50 % (Australian Pork Limited, 2013, Engblom et al., 2007). Such a high turnover rate has caused primiparous sows and GP to represent a large proportion of the herd, contributing significantly to overall productivity. Improving the performance of GP is therefore imperative to reduce the burden of having these animals in the herd. A thorough understanding of the underlying biological basis for differences between GP and SP is necessary for developing interventions to improve the performance of GP.

The purpose of this review is to summarise the published literature investigating the growth, health status, value and reproductive performance of GP in comparison to SP. Furthermore, it aims to identify sow and piglet factors that could be targeted to the overall productivity of GP on farm.

The primiparous sow and her progeny

Growth performance – at birth, and before and after weaning

Birth weight is an important determinant of subsequent performance in pigs (Dunshea et al., 2003). Most studies have reported that GP are born significantly lighter than SP and continue to be lighter at all stages of their productive lifetime. The magnitude of this disparity can vary in the literature due to factors such as different genetics, feeding and nutrition, the parity of the multiparous sows included in the study, and the time of year. Regardless, GP are consistently reported as lighter than SP throughout the literature with differences ranging from 200 to 250 g lighter, on average (Miller et al., 2012a, Carney-Hinkle et al., 2013, Ocepek et al., 2016, Craig et al., 2017a, 2017b, and 2019d, Gonzalez-Añover and Gonzalez-Bulnes, 2017, Ison et al., 2017, Vallet and Miles, 2017), with a higher proportion of low birth weight (**LBW**) piglets (<1.1 kg) born to primiparous sows (Wijesiriwardana et al., 2019).

Parity structure is a major factor affecting the magnitude of this difference, with the largest average piglet birth weight discrepancy occurring between parities 1 and 2 (Freking et al., 2016, Vallet and Miles, 2017) with parity 1 sows having the lighter piglets. This may be due to increases in litter sizes (Foxcroft et al., 2006) and with an increased focus on gilt management in recent times, emphasising selection for high growth rates resulting in gilts reaching puberty earlier (Rozeboom, 2015) and possibly maturing more rapidly between parities 1 and 2. Regardless, a large difference between birthweights of GP and SP is observed in multiparous sows up to parity 4. Generally, it appears that when older sows (parity $\geq$ 5) are included in analyses, the difference between GP and SP birth weight is lower (Muns et al., 2015, Zotti et al., 2017, Mallmann et al., 2018), indicating that GP and SP from parity $\geq$ 5 sows may have similar average birth weights (Da Silva et al., 2013). The most likely reason for the similar average birth weights seen between GP and SP from older sows is within-litter birth weight variation. Within-litter birth weight variation increases with parity (Zotti et al., 2017), likely due to uterine crowding and disproportionate growth in SP litters with higher litter sizes (Quiniou et al., 2002, Da Silva et al., 2013) resulting from a higher ovulation rate with increasing parity (Foxcroft et al., 2006).

Parity differences in preweaning growth and weaning weight follow a similar pattern to birthweight, whereby progeny from younger multiparous sows (parities 2 and 3) have higher preweaning growth than those from primiparous and higher parity sows (Neil, 1999; Solanes et al., 2004; Zotti et al., 2017). Milk yield seems to be the main determinant of preweaning growth and since primiparous sows are thought to have a significantly lower milk yield than multiparous sows (Hansen et al. 2012), it is intuitive that this would cause poorer growth in GP before weaning (Ferrari et al., 2014). In a study by Smits and Collins (2009), SP that were reared by primiparous sows gained significantly less weight than SP that were reared by multiparous sows in the preweaning period in agreement with the notion that milk production in primiparous sows is inadequate for optimum preweaning growth. However, these authors concluded no net benefit in piglet weight gain as improvements in GP reared by multiparous sows were negated by losses in SP reared by primiparous sows.

The literature indicates that GP are significantly lighter than SP at weaning, and total litter weights are substantially lower for primiparous sows at weaning due to lower litter sizes and total litter weight gain (Vallet et al., 2015; Terry et al., 2015). However, the average weaning weights of GP in comparison to SP are difficult to determine from the literature due to the confounding effect of weaning age. This is reflected in the range of weight differences published between GP and SP, from 200 g (Pettigrew et al., 1986) to approximately 2 kg (Craig et al., 2017a; 2019d). Furthermore, Ocepek et al. (2016) reported 'total maternal litter investment', defined as litter weaning weight, plus weight of all stillborn and mummified foetuses and weight of all piglets that died preweaning, was significantly lower in primiparous sows compared to multiparous sows.

Gilt progeny continue to exhibit poorer growth after weaning when compared to SP (Wijesiriwardana, et al. 2020). Interestingly, feed intake is similar between GP and SP during the first week after weaning (Wijesiriwardana et al., 2020). However, SP consumed more feed during the subsequent weeks of weaning in this study. Miller et al. (2012a) also reported a lower feed efficiency in GP compared to SP. Collectively, this suggests that GP recover from the effects of weaning at a slower rate than SP. Indeed, Craig et al. (2017a) found that, although most of the growth differences between GP and SP in later life could be attributed to a lighter weaning weight in GP (Fig. 1A), they still grew slower than SP from weaning up until 10 weeks of age, even after accounting for weaning weight differences. This finding was later corroborated in a follow-up study by the same authors in a different farming system with pigs from an unrelated genetic source (Fig. 1B; Craig et al., 2019d). However, these studies did strongly suggest that if GP and SP could be weaned at similar weights, the difference between their weights at sale could be minimised.

Mortality and morbidity

Findings from studies are inconsistent with regard to the differences in the incidence of prenatal mortality (stillbirths and mummified foetuses) between GP and SP. However, Ocepek et al. (2016) and Jang et al. (2017) reported similar prenatal mortality between primiparous and multiparous sow litters, but with less total piglets born in primiparous sows, which may indicate that the proportion of piglets born dead may be higher in these litters.

It has been reported that GP have higher preweaning survival rates than SP (Li et al., 2012a, Miller et al., 2012a, Muns et al., 2015, Vallet and Miles, 2017), but other studies have reported no

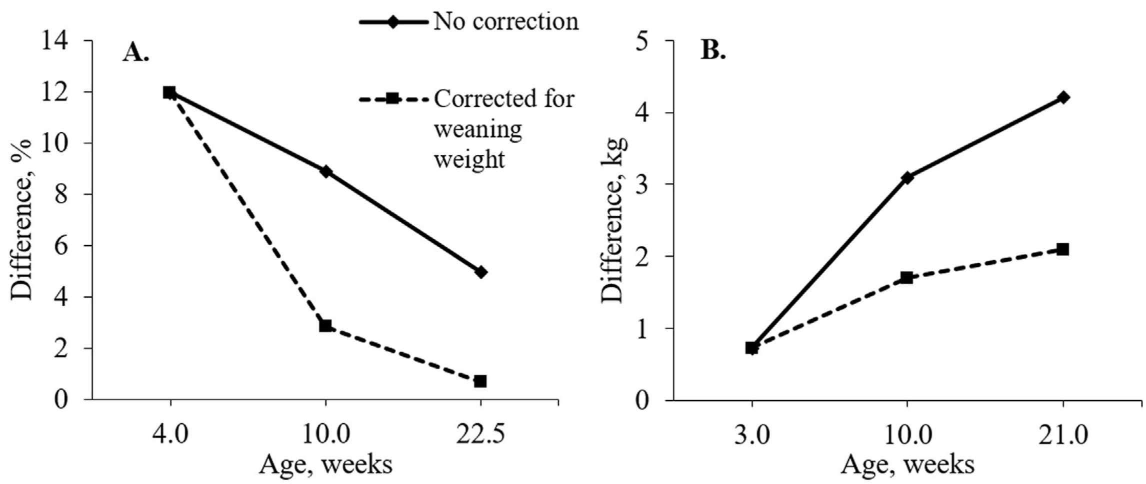

Fig. 1. Differences in gilt (GP) and sow progeny (SP) weights after weaning with and without a correction for weaning weight, in terms of percentage difference (A; source Craig et al., 2017a) and absolute difference in kg (B; source Craig et al., 2019d).

such differences (Milligan et al., 2002, Gatford et al., 2010, Freking et al., 2016). Sow progeny have higher rates of mortality compared to GP in the early high-risk period in the first 3–7 days of life (Mahan, 1994). In this period, early colostrum intake is vital to newborn piglets, especially those of LBW, as they are particularly prone to hypothermia (Le Dividich et al., 2005). Additionally, crushing is the predominant cause of these deaths in SP in this period (Mahan, 1994, Miller et al., 2012a). Few studies analyse preweaning mortality from 3 days of age to weaning, with these studies often reporting contradictory results. For example, Edwards et al. (2013) and Craig et al. (2019c) reported higher mortality in GP than SP while Miller et al. (2012b) and Craig et al. (2021) reported no differences in this period. These differences may have been impacted by parity; for example, primiparous and parity two sows have similar rates of total preweaning mortality in their litters (Milligan et al., 2002, Koketsu et al., 2006, Freking et al., 2016). It is also often not reported whether the effect of biological or rearing parity is being referred to in each study. It may be that the rearing dam parity does not affect preweaning survival in the same way as it does growth performance (Miller et al., 2012a, Ferrari et al., 2014). However, it has recently been shown that the parity of the rearing dam may impact the preweaning survival chance of fostered piglets (Harper and Bunter, 2019). Nonetheless, as studies are usually not primarily designed to test parity differences in preweaning mortality, sample sizes and statistical power are often lacking to detect parity effects.

Interactions between dam parity, litter size, and individual piglet birth weight greatly impact a piglet's risk of dying before weaning (Roehe and Kalm, 2000, Muns et al., 2015). Other confounding influences that may impact preweaning mortality include herd health status (Friendship and O'Sullivan, 2015), season (Koketsu et al., 2006), sow age and genotype (Roehe and Kalm, 2000), gestation and (or) farrowing environment (Li et al., 2012b, Jang et al., 2017), gestation (Roehe and Kalm, 2000) and (or) lactation length (Koketsu et al., 2006), sow feed intake and other management factors (Galiot et al., 2018), which all may interact with sow parity. The ways that these factors interact with parity to impact preweaning mortality is poorly understood and requires further investigation.

Differences between GP and SP mortality rates after weaning are seldom reported although it seems GP may have a higher risk of dying in the immediate postweaning period (Holyoake, 2006, Miller et al., 2012b, Craig et al., 2017a). However, some studies showed no difference in mortality between GP and SP in this period (Larriestra et al., 2006, Miller et al., 2012a), and records on mortality differences in the grower-finisher period are scarce. Gilt progeny have higher morbidity resulting in higher rates of medication (Holyoake, 2006, Miller et al., 2012b) and removal from the herd due to poor body condition or illness (Miller et al., 2012b) than SP after weaning. A higher prevalence of respiratory-related mortality has been reported in GP in both the nursery (Edwards et al. 2013) and the grower-finisher periods (Craig et al. 2017a). These observations suggest that GP have a higher susceptibility to illness, which can be attributed to an interplay of factors such as LBW and reduced humoral immune responsiveness due to lower colostrum consumption (Miller et al., 2012a). These factors will be discussed later in this review. Furthermore, various studies have reported that GP have higher rates of medication (Holyoake, 2006, Craig et al., 2017a) and mortalities (Holyoake, 2006, Miller et al., 2012a) after weaning, and that GP are at a higher risk of lameness than SP (Calderón Díaz et al., 2017). However, this finding was not corroborated in the study by Miller et al. (2012a).

Sale weight and carcass characteristics

Direct comparisons between GP and SP in terms of their growth to sale and carcass characteristics are limited in the peer-reviewed literature. However, it is widely accepted that GP take longer to reach market weight and contribute to a larger proportion of the variation between carcass weights and carcass quality encountered at sale, impacting overall profitability. This was proposed by Schinckel et al. (2010) who predicted from a series of models that GP were 4.9–5.7 kg lighter at 150 days of age, took 6.2–7.5 additional days to reach a saleable weight of 125 kg, and had a 4.5 kg lighter carcass than that of progeny born to multiparous sows of parities 2–6. This was similar to previous studies that report GP weighing 4.2–4.6 kg lighter than SP at sale at around 21–22 weeks of age (Craig et al., 2017a; 2019d). Tummaruk et al. (2000) reported that backfat depth in breeding gilts born to primiparous sows was significantly lower than those born to multiparous sows at 100 kg live weight, but this was not corrected for age and the largest difference was 0.2 mm between GP and SP from parity five sows. Indeed, it has been shown recently that P2 backfat was not different between GP and SP at sale when adjusting for carcass weight (Craig et al., 2017a; 2019d), with both groups in these studies sold at a similar age.

Calderón Díaz et al. (2017) reported that carcasses of GP had a 1 % lower lean meat percentage than SP. However, this difference was not statistically significant, and GP had the numerically highest cold carcass weights compared to SP from sows of parity 2–6 at 24 weeks of age. Live weight differences at sale between GP and SP were not reported in that study. Da Silva et al. (2013) found that GP had a lower number of secondary muscle fibres at birth than SP from sows up to parity 4, as well as a lower semitendinosus muscle weight and area, which may lead to lower muscling of the carcass at sale age. However, previous studies have shown no difference in loin depth at the P2 site in GP carcasses compared to those of SP (Craig et al., 2017a; 2019d).

Further investigation into these differences is necessary to determine the exact impact of the inclusion of GP in commercial herds, to conduct benefit-cost analyses to assist producers in making management decisions of numbers of GP bred and how these animals are managed to maximise their performance to slaughter.

Reproductive performance of gilt progeny

Gilt growth rates, P2 backfat, and degree of loin muscle depth at selection and (or) breeding may also impact reproductive performance in breeding gilts. Indeed, GP bred as breeding herd replacements have a higher P2 backfat at selection (at 24 weeks of age) than SP, when correcting for live weight (Craig et al., 2017b), which may indicate a higher propensity for these animals to deposit fat compared to muscle. This, coupled with their slower growth rates, may impact their reproductive performance as breeders.

Birth weight and colostrum intake can also influence reproductive development and, therefore, performance in the breeding herd, and this may provide information about the reproductive performance of GP relative to their SP counterparts. Low birth weight is associated with poorer reproductive development and performance in breeding females measured by the removal due to anoestrus and piglets born alive in the first farrowing (Magnabosco et al., 2015; 2016, Almeida et al., 2017). Furthermore, boars that were lighter at birth were shown to have reduced testicular development (Smit et al., 2013), smaller testes size and produce 34 % fewer semen doses in their lifetime compared to high birth weight boars (Auler et al., 2017).

Components of colostrum and milk have also been identified as having a major role in the early development of the reproductive system in gilts (Bagnell et al., 2017, Bartol et al., 2017) and boars (Rahman et al., 2014) in a phenomenon known as the 'lactocrine hypothesis'. Colostrum and milk contain hormones such as relaxin and prolactin (Bartol et al., 2008) and growth factors such as IGF-I and IGF-II (Xu et al., 2000) that assist in the development of reproductive organs such as the ovaries, uterus, mammary glands, testes and male accessory sex glands (Bartol et al., 2008; 2017, Rahman et al., 2014, Bagnell et al., 2017). Accordingly, colostrum intake in piglets, measured as plasma immunocrit ratio 24 h after birth, has been negatively correlated with age at puberty and first mating and positively correlated with litter size in breeding females (Vallet et al., 2015).

Researchers have recently focused on understanding the differences in reproductive performance between GP and SP in commercial breeding herds. Such differences in reproductive performance may arise due to lower average birth weights in GP and interruptions in colostrum and milk supply and consumption (discussed further below) in these animals compared to their SP counterparts. It has been shown that GP selected for breeding are 1 day older at first mating than their SP counterparts (Craig et al., 2017b, Hewitt et al., 2017). Craig et al. (2017b) found GP were more likely to be removed between selection and first breeding for reproductive reasons such as failing to show oestrus before 220 and 270 days of age. However, once they had been bred, GP were more likely to maintain pregnancy, with a significantly higher farrowing rate in the first parity than SP. Contrary to these findings, Hewitt et al. (2017) saw no difference in removals between GP and SP in the breeding herd, which may indicate that these differences are dependent on genetic lines used. Whereas no differences were found in reproductive performance between GP and SP up until parity 3 in the study of Craig et al. (2017b), Hewitt et al. (2017) found that GP having their first litter had a significantly higher proportion of stillborn piglets per litter and an extended wean to oestrus interval between parities 1 and 2 compared to SP. However, both authors agreed that there is insufficient evidence to simply not select GP for breeding. This group shows the most potential for genetic improvement as they represent an additional breeding generation and may accelerate genetic gain within the breeding herd. While there is no difference in sow longevity to parity 3 between GP and SP in breeding herds (Craig et al., 2017b), it is of interest to investigate lifetime longevity differences between these progeny groups in future studies.

Factors impacting gilt progeny health, performance, and overall profitability

Sow factors

Reasons for poorer performance of GP are complex and multifaceted but can largely be attributed to the gilt herself. Gilts are mated at a young age, and this can have significant consequences on metabolism during gestation and lactation. During gestation, gilts must partition dietary nutrients into critical processes such as mammary gland development, uterine, placental, and foetal growth, while also supporting their own body growth (Thomas et al., 2018a; 2018b). During lactation, gilts preferentially partition energy into their own growth rather than milk production (Pluske et al., 1998), which in turn can also limit the production performance of GP. This section summarises the physiological demands placed on the gestating and lactating gilt in detail.

The primiparous sow during gestation

The gilt is first mated at a physiologically young age, usually between 220 and 270 days, and typically at her second or third observed oestrus. However, due to the ongoing growth and development of the gilt at this age, dietary energy and vital nutrients are partitioned into her own growth during gestation (Whittemore, 1996), resulting in less energy and fewer nutrients being available to support the critical processes of pregnancy (Fig. 2). Approximately 30 % of weight gain during gestation in primiparous sows is attributed to the growth of the sow herself (Ji et al., 2005) rather than the development of the foetuses or mammary glands. This continued demand thereby necessitates a higher relative maintenance requirement for primiparous sows than for older sows (Everts and Dekker, 1995). However, energy partitioned into growth of the conceptuses is still of higher priority than maternal body weight gain in primiparous sows (Everts and Dekker, 1995, Ji et al., 2005).

In this regard, Thomas et al. (2018a) reported that primiparous sows increased their body weight in each period of gestation in their study, whereas the live weight of dams of parities 2 and >3 remained static from days 75 to 109 (Fig. 3). Furthermore, primiparous sows have a greater proportional maintenance requirement from day 75 to day 109 of gestation compared to multiparous sows (Thomas et al., 2018a). This suggests that foetal growth in primiparous sows may be compromised during late gestation due to the preferential partitioning of nutrients and energy towards their own growth.

Placental sufficiency may indicate how well the sow allocates energy and nutrients to foetal development. Town et al. (2005) reported that placental sufficiency (the ratio of placental weight

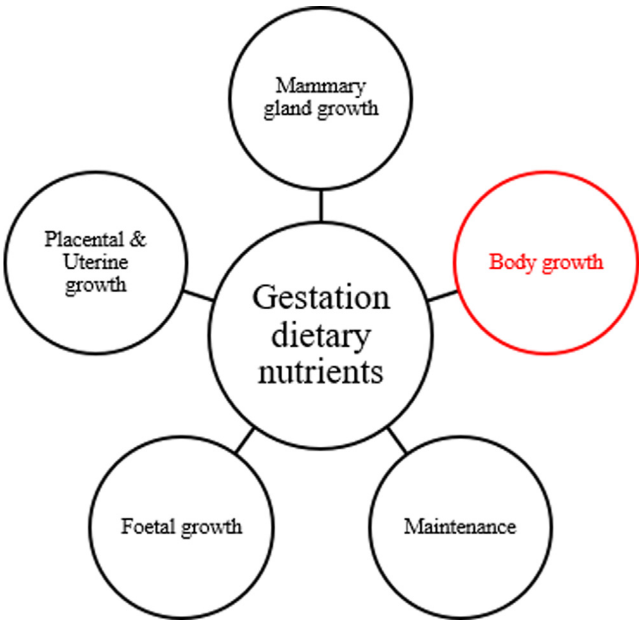

Fig. 2. Key metabolic processes of gestation in the primiparous sow (Feyera and Theil, 2017).

to foetal weight) was higher in parity 2 and parity 3 sows at day 90 of gestation compared to primiparous sows, that decreased again in older sows. However, no difference was observed in overall placental weights between primiparous and multiparous sows at day 50 of gestation (Gatford et al., 2009) or at term (van Rens and van der Lende, 2004), which suggests that placental insufficiency may not be responsible for differences in prenatal development between GP and SP. From these equivocal results, it is clear that further work is required in this area.

The primiparous sow during farrowing and the transition period

The parity of the sow can impact the farrowing process. Primiparous sows have a narrow birth canal since they have not experienced a prior farrowing (Pejsak, 1984; Vanderhaeghe et al., 2013). On the other hand, older sows (parity ≥ 5) have reduced uterine muscle tone and hence farrowing duration can be prolonged (Vanderhaeghe et al., 2013). Piglets in these situations can be asphyxiated and may be less vital at birth or be stillborn (Alonso-Spilsbury et al., 2007). Generally, primiparous sows are observed to have a shorter farrowing duration than multiparous sows (Tummaruk and Sang-Gassanee, 2013). While a longer farrowing duration in multiparous sows is associated with a higher rate of stillbirth, this is not the case for primiparous sows who take a shorter time to complete farrowing but still give birth to a high proportion of stillborn piglets (Cutler et al., 2006; Vanderhaeghe et al., 2013). In these younger sows, the narrow birth canal is the main reason for an increase in stillbirth rates (Pejsak, 1984).

Primiparous sows have also been shown to exhibit more aggressive behaviour towards piglets, resulting in death or serious wounds, compared to multiparous sows (Alonso-Spilsbury et al., 2007). Stress induced by the farrowing process can lead to aggression and restlessness in primiparous sows that may experience a higher level of stress and pain compared to older sows (Thodberg et al., 2002). Furthermore, primiparous sows exhibit fewer maternal behaviours such as nest building than sows that have previously experienced farrowing and lactation (Thodberg et al., 2002). However, Ocepek and Andersen (2017) recently found no effect of parity (primiparous vs multiparous; parities 2–6) on nest building activity, communication between the dam and her piglets or 'protectiveness' of the dam in an individual loose-housed farrowing system, all of which had a substantial impact on piglet survival in that study.

A major cause of mortality in postnatal piglets is crushing from the sow, or 'overlaying' (Alonso-Spilsbury et al., 2007). The incidence of crushing is more frequent in litters of older parity sows with a high degree of litter variation (Weary et al., 1998) and may be secondary to other health issues affecting the viability of the piglet, and therefore its capacity to escape before being overlain (Alonso-Spilsbury et al., 2007). Even though primiparous sows seem to have more piglets born classed as LBW than multiparous sows (Wijesiriwardana et al., 2019), a higher proportion of SP born to older parity sows are born at very LBWs (i.e. parity ≥ 6; Milligan et al., 2002), and this may likely contribute to a higher incidence of crushing in these litters, because piglets with low average weight gain that have consumed less milk spend more time at the udder

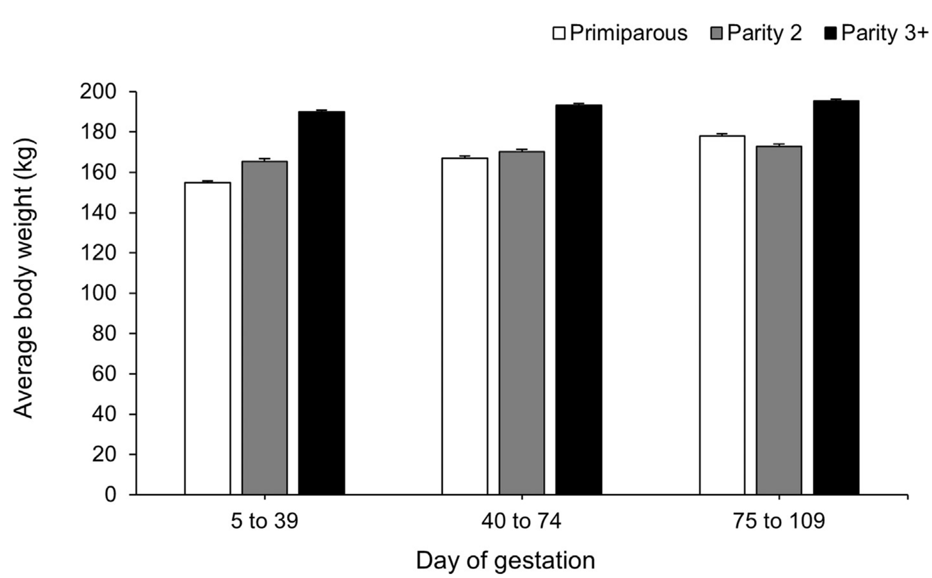

Fig. 3. The average BW (kg) of primiparous sows and sows of parities 2 and 3 + during three periods of gestation in days (Thomas et al., 2018a).

and near the sow in search of milk (Weary et al., 1998). The larger size of the older sow would reduce the free area of the farrowing crate available for the piglet to escape.

The difference in frequency and type of postural changes between primiparous and multiparous sows may also affect the probability that a piglet is crushed. Uncontrolled body movements and postural changes in sows increase the incidence of crushing (Damm et al., 2005), and the larger physical size of older parity sows may result in them having difficulty controlling their posture changes in a confined space such as a farrowing crate (Thodberg et al., 2002, Li et al., 2012a, Ison et al., 2017). This may also impact teat access for piglets. It has been reported that primiparous sows may purposefully impede the nursing of their piglets, especially when stressed around parturition (Thodberg et al., 2002, Alonso-Spilsbury et al., 2007). Contrarily, the number of postural changes increases the time to first suckle for newborn piglets (Rohde Parfet and Gonyou, 1990), and the interval between nursing and milk ejection was longer in older parity sows (Fraser and Thompson, 1986). Teats may be more accessible to piglets nursing primiparous sows because they spend more time lying laterally than older sows (Ison et al., 2017), and higher parity sows, with more pendulous udders, find it difficult to expose the bottom row of teats when nursing (English et al., 1977).

Mammary development

Maternal age can significantly impact mammary development, udder morphology, and uptake of nutrients into the mammary gland. The mammary glands continue to grow and develop as sows age with differences in udder morphology observed over several parities (Balzani et al. 2016a, Farmer and Hurley, 2015). The process of mammary development differs between primiparous and multiparous sows, with a proportionally higher increase in mammary volume during lactogenesis in primiparous sows, as a result of both cellular hyperplasia and hypertrophy (Farmer and Hurley, 2015). In contrast, this process occurs due to hypertrophy alone in multiparous sows. Udder morphology can influence teat access and piglet latency to the first suckle and total colostrum and (or) milk intake (Vasdal and Andersen, 2012, Balzani et al., 2016a). Mammary development is more uniform across the udder in primiparous sows, with discrepancies in teat size and weight between posterior and anterior teats more pronounced as parity advances (Dyck et al., 1987, Nielsen et al., 2001). Multiparous sows have a lower proportion of functional teats (Vasdal and Andersen, 2012) and more variation in milk production between teats (Fraser and Thompson, 1986). Furthermore, smaller piglets do not suckle as vigorously as larger piglets (King et al. 1997), which can fail to stimulate oxytocin and therefore maintain hormonal feedback loops, reducing milk let-down in the teat they are suckling (Cabrera et al., 2012).

Colostrum production and composition

Due in part to the effects of maternal age on mammary development and the endocrine control of lactation, the production and composition of colostrum and milk are also greatly influenced by dam parity. Likely, compromised growth and health in GP are partially due to the capacity of the primiparous sow to produce colostrum, the intake of colostrum by the piglet and its ability to suckle, and possibly the colostrum composition in primiparous sows, in particular the concentrations of macronutrients and immunoglobulins, all of which affect energy metabolism, gastrointestinal tract (**GIT**) development, and acquisition of maternal immunity in progeny.

Colostrum yield varies greatly among sows (Devillers et al., 2007, Foisnet et al., 2010), with differences reported in the literature between primiparous and multiparous sows being equivocal (Quesnel et al., 2015). Primiparous sows have lower serum prolactin and oxytocin concentrations than multiparous sows before farrowing (Quesnel et al., 2013), which may cause reduced colostrum and milk yields (Foisnet et al., 2010) as lactation is initiated by a sudden decrease in progesterone and resultant prepartum surge in prolactin (Farmer et al., 2006). Farmer et al. (1995) found similar serum prolactin concentrations between primiparous and multiparous sows 24 h after farrowing, and higher progesterone concentrations in primiparous sows, suggesting a lower prolactin-progesterone (PRL/P4) ratio in primiparous sows around farrowing. A higher PRL/P4 ratio around farrowing is correlated with higher colostrum yield (Loisel et al., 2015). Collectively, this indicates that colostrum yields are lower in primiparous sows. However, the colostrum yields reported in the literature vary. For example, primiparous sows are reported to have a lower colostrum yield than higher parity sows (Devillers et al., 2007, Ferrari et al., 2014, Nuntapaitoon et al., 2019) with the highest colostrum yields occur in parity 2 and parity 3 sows (Devillers et al., 2007, Decaluwe et al., 2013, Nuntapaitoon et al., 2019). Others have reported that colostrum yield was not different between parties at all (Quesnel, 2011, Declerck et al., 2015).

Assessment of colostrum yield may depend on the measurement method used, which can be done through the weigh-suckle-weigh, deuterium oxide dilution techniques or via published equations based on piglet growth rate (Theil et al., 2014, Quesnel et al., 2015). Comparisons of individual piglet colostrum intake between GP and SP are not common, primarily because colostrum intake being difficult to measure directly (Theil et al., 2014). In a study by Ferrari et al. (2014), colostrum yield was measured using a regression equation relating colostrum intake and piglet weight gain. These authors reported that colostrum availability per piglet in primiparous sow litters was substantially lower than that in multiparous sow litters, and suggested this may be attributable to a lower total colostrum yield from these sows. This is understandable considering individual colostrum intake generally increases with increasing birth weight (Devillers et al., 2007, Quesnel, 2011).

Concentrations of immunomodulatory factors in colostrum are likely impacted by the level of antigen exposure of the dam. Intuitively, older animals have been exposed to a higher number and range of pathogens and have had more time to develop their immune competence (Friendship and O'Sullivan, 2015). This suggests that primiparous sows at the time of gestating and nursing their first litter are more immunologically naïve than more mature multiparous sows. Furthermore, this first farrowing marks their exposure to a new, unfamiliar environment (i.e. the farrowing house) and a new group of potentially unfamiliar pathogens. This becomes particularly important in determining the maternal transfer of humoral immunity to their piglets soon after farrowing. This increased pathogenic challenge in younger, more naïve primiparous sows may contribute to reduced transmission of maternal immunity to their offspring through colostrum, affecting the ability of these progeny to mount their own immune response to pathogenic challenges in the suckling period and beyond (Le Dividich et al., 2005). Indeed, total serum immunoglobulin concentrations increase with advancing age in breeding sows (Klobasa et al., 1985), which is also reflected in an increase in total serum protein and a lower albumin to globulin ratio in multiparous sows compared to primiparous sows (Verheyen et al., 2007).

Results from studies comparing colostrum immunoglobulin G (**IgG**) concentrations are equivocal. For example, Inoue et al. (1980) and Klobasa and Butler (1987) observed increasing IgG concentration with parity, while Cabrera et al. (2012) observed lower IgG concentrations in primiparous sows compared to multiparous sows of parities 2–8. Quesnel (2011) reported that IgG concentrations are the highest in parity 5 or greater sows. However, most recent studies have reported that colostrum IgG concentrations are more similar between parities (Kielland et al., 2015, Balzani et al., 2016b, Hasan et al., 2016, Ison et al., 2017, Craig et al., 2019a, Segura et al., 2020). The discrepancy between studies may be a result of the range of parities used which may affect the mean concentration of colostrum IgG reported in these studies.

Immunoglobulin G is usually the predominant isotype studied. However, in terms of other immunoglobulins, earlier studies have reported lower that primiparous sow colostrum has the lowest IgA concentration (Klobasa et al., 1986) and the highest IgM concentration (Inoue, 1981) concentrations compared to multiparous sows. Furthermore, Klobasa and Butler (1987) found that while IgM colostrum concentrations were broadly similar across most parities, they were especially highest in older sows. Although these differences are not well studied in the present literature, lower IgA and IgM concentrations in primiparous sow colostrum may have several implications for the performance of GP, and this demands further study. A reduction in IgA acquired by the piglet may interact with establishing the GIT microbiome (Carney-Hinkle et al., 2013), and de novo synthesis of immunoglobulins by the piglet may be affected (Klobasa et al., 1986). Immunoglobulin M is the initial antibody secreted by B cells in response to antigen challenge and a reduction in acquired IgM may result in a lowered ability to respond to antigen challenge. Furthermore, Forner et al. (2021) recently showed that colostrum from multiparous sows, in comparison to that from primiparous sows, contained a higher concentration of T lymphocyte subsets important for neutralising antigens and promoting cellular immune responses in the young piglet (namely central memory $CD4^{+}T$, effector memory $CD4^{+}T$, and central memory $CD8^{+}T$ cells).

Discrepancies between studies in terms of parity differences in colostrum and milk composition may be as a result of genetic differences (Szyndler-Nędza, 2016, Picone et al., 2018), season (Picone et al., 2018), vaccination and medication (Mainau et al., 2016), and (or) nutrition (Quesnel et al., 2012). Colostrum and milk composition, especially that of IgG concentrations, can also vary widely depending upon the timing of sample collection (Theil et al., 2012), udder section sampled (Inoue et al., 1980), oxytocin administration (Farmer et al., 2017), and farrowing induction (Vallet and Miles, 2017).

The macronutrient profile of colostrum is relatively poorly studied compared to that of mature milk, and reports are equivocal in regard to differences in some constituents between primiparous and multiparous sows. The total concentration of fat in colostrum is the highest in primiparous sows and decreases after parity 1 (Declerck et al., 2015, Szyndler-Nędza, 2016, Craig et al., 2019c, Segura et al., 2020). Colostrum protein concentration is similar between primiparous and multiparous sows in most studies (Declerck et al., 2015, Szyndler-Nędza, 2016, Craig et al., 2019c; 2019d), while lactose concentrations were lower in primiparous sows in some studies (Szyndler-Nędza, 2016) and similar to that of multiparous sows in others (Declerck et al., 2015, Picone et al., 2018), which may be impacted by sampling time (Craig et al., 2019a, Segura et al., 2020). Collectively, the majority of these studies suggest that most aspects of the macronutrient profile are similar between the primiparous and multiparous sow. Therefore, the disparity between the early life performance of their progeny is likely not affected by the macronutrient profile of milk.

The effects of parity on the concentrations of growth factors and other bioactive factors in colostrum have also been poorly studied. Insulin-like growth factor I (IGF-I) concentrations in colostrum from primiparous sows were lower than that of sows from parity 3 onwards (Averette et al., 1999) but equal to that of parity 2 sows (Monaco et al., 2005). However, there were higher concentrations in colostrum from parity 2 sows compared to parity 1 sows in the latter study. More clarification is warranted to understand how these possible differences may impact the early development of the GIT and other tissues in GP. Recent studies investigating the metabolomic profiles of colostrum from sows of different parities have reported that, overall, these profiles were largely similar between primiparous and multiparous sows (Luise et al., 2020, Keel et al., 2021), but subtle differences in some important metabolites may be impacting performance differences between GP and SP. This, also, warrants further investigation.

Lactation feed intake

Lactation can be a highly catabolic period where the dam mobilises labile body fat and protein to support milk production. However, due to the continued selection for leanness, primiparous sows often enter lactation with less labile tissue to support milk synthesis than older sows (Whittemore, 1996). As a consequence, this reduces the energy and other nutrients available for the piglet. Several studies have reported significantly lower lactation feed intake in primiparous sows than multiparous sows (Gatford et al., 2010, Ocepek et al., 2016). Yang et al. (2009) reported that primiparous sows ate 230 g/day less than multiparous sows in lactation, whereas more recently, Mallmann et al. (2018) reported this difference to be much higher at 1 740 g/day. Discrepancies between studies may be affected by lactation length or the multiparous sow parities used, as feed intake increases with advancing parity (Mahan et al., 2000, Jang et al., 2017). The largest increase in lactation feed intake occurs between parities 1 and 2, increasing more gradually from parity 2 onwards (Mahan, 1994, Mahan et al., 2000) with no difference observed in the first week of lactation (Gatford et al., 2012, Ison et al., 2017). Several studies have demonstrated that feed intake during lactation by primiparous sows is often insufficient for adequate milk production (Whittemore, 1996, Pluske et al., 1998). Even when primiparous sows were super-alimented via a gastric cannula with feed at 125 % of their maximum feed intake, they directed almost all of the additional absorbed nitrogen towards their maternal reserves rather than milk production (Pluske et al., 1998). This is in contrast to multiparous sows that direct extra nutrients into maternal growth and milk production. When feed offered to lactating primiparous sows is restricted, they mobilise maternal labile body tissue to maintain milk production, resulting in reduced growth of their litter (Pluske et al., 1998).

Adult sows have an increased capacity to digest and absorb nutrients through the GIT than growing pigs (Le Goff and Noblet, 2001) and a longer transit time of ingesta (Varel, 1987), allowing more time for digestive and absorptive processes to occur. As such, two separate dietary energy values are recommended for growing and adult pigs when formulating diets (Le Goff and Noblet, 2001). Within sows, the smaller physical size of the primiparous sow is accompanied by a smaller size and length of the GIT, that in turn might cause reduced nutrient digestibility and absorption in the younger primiparous compared to older multiparous sow (Le Goff et al., 2002). Jacyno et al. (2016) reported that primiparous sows had a lower apparent total tract digestibility of dry matter, energy, organic matter, protein, and insoluble fibre compared to multiparous sows during gestation and lactation. Considering these differences, separate DE values could be considered for primiparous and multiparous sows. However, we are unaware of any specific data in relation to this proposition. Overall, the higher demand for energy for body growth in gestating and lactating primiparous sows impacts the availability of nutrients for digestion and (or) absorption, which may result in less nutrients available for efficient milk production and hence contribute to the reduced growth of their progeny.

The lower lactation feed intake of primiparous sows typically causes a greater catabolic state leading up to weaning. Primiparous sows lose more body condition (Ocepek et al., 2016) and greater proportions of their body weight (Peters and Mahan, 2008, Mallmann et al., 2018) and backfat (Yang et al., 2009, Jang et al., 2017) in lactation compared to multiparous sows, indicative of entry into a catabolic state (Dunshea and D'Souza, 2003, Yang et al., 2009). These losses have implications for hormonal control of oestrus, with lower luteinising hormone (LH) pulse frequencies in primiparous sows compared to multiparous sows at farrowing and weaning (Yang et al., 2009) as well as lower basal circulating LH and follicle stimulating hormone (FSH) concentrations. Consequently, primiparous sows can experience a prolonged first wean to oestrus interval and sub-optimal reproductive performance in their second parity (Thaker and Bilkei, 2005).

Milk production and milk composition

Due to the primiparous sows' need to partition nutrients towards her own growth, nutrients are partitioned away from supporting the metabolically demanding process of lactation resulting in reduced milk yield (Fig. 4). Not surprisingly, milk yield typically increases as parity increases with primiparous sows producing less milk than multiparous sows (King, 2000, Beyer et al., 2007, Ngo et al., 2012), which concurs with lower growth rates of GP in lactation. In a meta-analysis of 21 studies measuring milk yield in sows, Hansen et al. (2012) concluded that there were no differences in milk yield between parities on day 5 or day 20 of lactation, but primiparous sows had the lowest yield on day 30. This could be as a result of lower suckling pressure due to lighter birth weights and litter numbers, or lower milk output in (likely catabolic) primiparous sows, who may have limited labile reserves at these later stages of a prolonged lactation, and may contribute excess energy to their own growth. Adjusting litters to a standard number and weight removed the effect of parity on milk yield in the study of Boyce et al. (1997), supporting the notion that lighter birth weights and lower litter numbers may contribute to this reduction in milk supply. The results of the study by Hansen et al. (2012) may also indicate that weaning age can influence differences in growth and development of GP and SP in early life. The largest increase in milk yield is between parities 1 and 2 (King, 2000), although

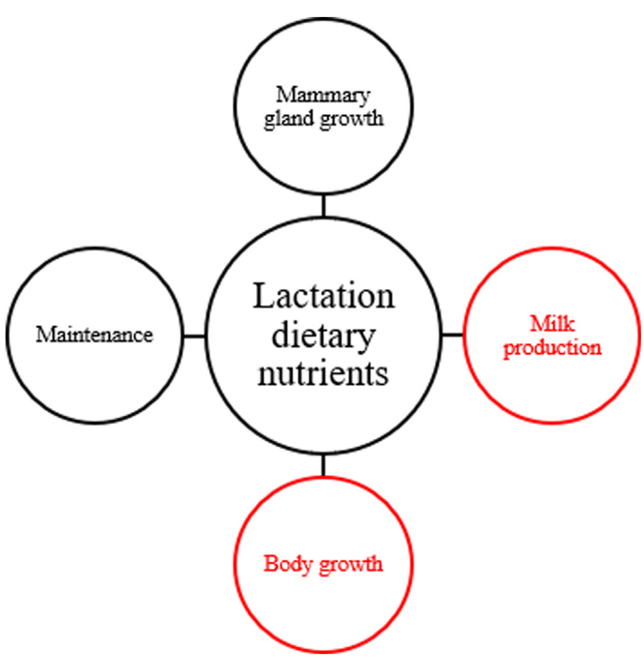

Fig. 4. Key processes of lactation in the primiparous sow. The metabolically demanding process of milk production often comes second when the primiparous sow is still contributing significant amounts of energy to her own growth (Feyera and Theil, 2017).

second-parity sows may still suffer from the energy demand of the first lactation (Gonzalez-Añover and Gonzalez-Bulnes, 2017), and hence, it is reasonable to conclude that this may impact their milk production. Hereafter, milk yield is the highest in parities 3 and 4 (King, 2000) and declines as sows reach parity 5 (Ngo et al., 2012).

If sufficient milk removal by piglets does not happen, then mammary involution occurs, and this cannot be reversed after 40 to 60 h of mammary regression (Theil et al., 2005). Primiparous sows are thought to impede suckling of their piglets, most probably as a result of inexperience (Alonso-Spilsbury et al., 2007), which may lead to premature involution of mammary glands. Furthermore, it has been shown that primiparous sows are more at risk of becoming ill soon after farrowing (Tummaruk and Sang-Gassanee, 2013), and this can disrupt lactogenesis. Indeed, Mahan (1994) and Mahan et al. (2000) found that younger sows, namely primiparous and parity 2 sows, had a higher incidence and severity of mastitis, metritis, agalactia syndrome than older sows. However, Gatford et al. (2010) found no difference in the incidence of lactation failure between primiparous and multiparous sows in their study.

The concentration of IgG in mature milk in regard to parity follows a similar pattern as colostrum (Klobasa et al., 1986). Fat concentrations typically fall as parity increases (Peters and Mahan, 2008, Declerck et al., 2015). Peters and Mahan (2008) reported a quadratic response of milk fat concentration to parity, increasing after parity 4. In contrast, a more recent study by Szyndler-Nędza (2016) observed no differences in milk fat concentrations between parities. Craig et al. (2019a) also reported no overall differences in total fat concentrations of milk. However, fat content was higher at day 3 of lactation in multiparous sows compared to primiparous sows. Milk fat concentrations may be highly variable depending on factors including the stage of lactation, nutrient intake, and breed (Hurley, 2015), which likely explains some of the conjecture in the literature.

Overall lactose and protein concentrations in milk are not affected by parity (Craig et al., 2019a, Quesnel et al., 2013, Declerck et al., 2015). However, studies comparing milk composition throughout the course of lactation are scarce. Beyer et al. (2007) measured milk comprehensively throughout lactation, milking 4 times per day from farrowing until weaning (28 days after farrowing). They found significantly lower protein and lactose concentrations in milk from primiparous sows compared to multiparous sows, and that the time-course of these changes over lactation was similar between parities. More recently, Szyndler-Nędza (2016) reported higher protein and lower lactose in milk from primiparous sows at day 14 of lactation compared to in parities 2 and 3, and concluded that milk composition was not repeatable in the same sow over consecutive parities. However, both Szyndler-Nędza (2016) and Craig et al. (2019a) observed lower concentrations of lactose in the milk of primiparous sows towards the end of lactation, with the latter attributing this to the inability of primiparous sows to keep up with the demands of milk production. These results suggest that differences in milk composition between sows of different parities are far more complex than first thought and require further investigation.

Piglet factors

Gilt progeny development in utero, at birth, and in the neonatal period

The majority of foetal growth occurs during the last third of gestation and is reflected in the weights of the conceptus (Thomas et al., 2018a; 2018b) and foetus (McPherson et al., 2004) during this time. In primiparous sows, conceptus weights have been reported to be lower than those of multiparous sows (Thomas et al., 2018a; 2018b). The differentiation in foetal weights between primiparous and multiparous sows occurs after day 50 of gestation (Gatford et al., 2009), with increases in protein accretion (0.25 to 4.63 g/day) and fat accretion (0.06 to 1.09 g/day) after day 69 of gestation (McPherson et al., 2004). However, the increased growth during late gestation coupled with the reduced birth weights of GP indicates that primiparous sows may have a lower uterine capacity. This has been suggested previously by Foxcroft et al. (2006) and offers a possible biological explanation for the reduced growth performance seen in GP.

Intrauterine growth restriction (IUGR) is defined by impaired growth and development of the foetus or its organs due to reduced blood flow, and transfer of nutrients and oxygen from the mother to the foetus (Wu et al., 2006). There is a scarcity of research investigating uterine capacity in the primiparous sow, but intuitively, it is plausible to suggest these young sows would have limited uterine capacity relative to multiparous sows. Furthermore, this may offer an underlying biological explanation as to why GP are born lighter and exhibit poorer growth throughout their lifetime. However, it must be noted that there is a clear distinction between LBW piglets and IUGR piglets, primarily due to the ability of LBW piglets to grow at an acceptable rate in later life given proper management (Edwards and Baxter, 2015). However, GP display some characteristics of IUGR such as asymmetric growth patterns in gestation that persist until weaning, suggesting that GP do not exhibit compensatory growth in lactation in the way other LBW piglets do in lactation (Craig et al., 2019b).

Asymmetric growth pertains to prioritisation of the development of organs of the nervous system such as the brain during early gestation and reduced weights of organs such as the liver, GIT tissue, and muscle mass, which develop later in gestation (McMeekan, 1940; Hammond, 1944; Bauer et al., 1998). For example, McPherson et al. (2004) observed GIT:foetal weight ratio increased as gestation progressed, which indicates that GIT growth accelerates towards the end of gestation. However, if uterine capacity is limited, this may restrict the growth of organs that develop later during gestation. Town et al. (2005) reported that parity affected brain:liver ratios with high ratios particularly seen in GP. Craig et al. (2019b) also reported this and increased brain:body weight, quadriceps weight:femur length, small intestinal weight:length and body weight:length ratios in GP. These findings suggest adequate development of the foetal nervous and skeletal systems in GP, which occurs during early gestation (Hammond, 1944). The discrepancies found between GP and SP in the study by Craig et al. (2019b) show that organ weights of body systems developed later in gestation such as the GIT or skeletal muscle may be compromised in GP. Collectively, these findings suggest that GP display many keys in utero development characteristics of IUGR.

The term IUGR is usually reserved for 'runt' piglets born to older parity sows with high litter sizes (Wu et al., 2006), where the asymmetric distribution of nutrients to each foetus occurs and usually results in 1 or 2 very small piglets at birth. However, it is plausible to suggest that all GP undergo some degree of IUGR, as the smaller uterine size of primiparous sows may act to limit the space available for conceptus growth, as well as the growth and functionality of the placenta (Town et al., 2005). A reduction in foetal glucose supply has been observed in cases of IUGR, and oxygen transfer to the foetus is also limited (Wu et al., 2006). These effects may have a lasting influence on piglet metabolism (Foxcroft et al., 2006), intestinal morphology, and enzymatic digestion processes (D'Inca et al., 2010).

The lighter weight of GP at birth may have several negative implications for their lifetime performance. Generally, the lighter a piglet is at birth then the greater is its surface area to volume ratio, and as it will have proportionately less fat and glycogen stores, thermoregulation is more problematic soon after birth (Rooke and Bland, 2002). Consequently, birth weight shows a strong negative correlation to preweaning survival (Fix et al., 2010). Typically, piglets born very light (often < 800 g) are usually classified as suffering from IUGR resulting in asymmetrical foetal development, as discussed earlier, affecting their morphology at birth and hence their ability to adapt to extrauterine life. Furthermore, several studies have shown that piglets born lighter have fatter carcasses (Gondret et al., 2006, Collins et al., 2007, Rehfeldt et al., 2008), poorer meat quality in regard to pH and drip loss (Rehfeldt et al., 2008), and reduced lean growth and meat tenderness due to a change in distribution and size of primary and secondary muscle fibres (Quiniou et al., 2002, Gondret et al., 2006), in comparison to their heavier counterparts. As previously mentioned, these differences in development caused by differences in foetal development and hence birth weight between GP and SP may impact their comparative lifetime performance.

Colostrum consumption and early immune function in gilt progeny

One of the distinct features of the neonatal piglet intestine is its ability to absorb colostral immunoglobulins, namely IgG. The acquisition of passive immunity via colostrum consumption is imperative to developing early immunity and survival due to the immunological naivety of the newborn piglet (Varley et al., 1987; Rooke and Bland, 2002). The transfer of intact IgG across the GIT occurs within a short time window in the neonatal intestine, somewhere in the first 18 to 36 h of life (Weström et al., 1984). Consequently, the passage of IgG across the intestinal epithelium in the neonatal period is a critical factor in determining piglet survival and establishing immunity in the piglet (Cabrera et al., 2012).

Differences in early immunological development between GP and SP have not been well characterised. The most common observation used to compare immune competence between the two progeny groups, especially before weaning when colostrum intake is the main source of piglet immunity, is through serum or plasma IgG concentrations. The circulating IgG concentration, the predominant immunoglobulin in pig colostrum, is a good indicator of colostrum intake and a higher chance of survival before weaning (Rooke and Bland, 2002). A method for the measurement of blood immunocrit ratio was developed by Vallet et al. (2013) and was shown to be positively correlated to serum IgG concentration and an increased chance of preweaning survival. This method is therefore gaining traction to measure immunity and predict mortality rate in piglets before weaning.

It is generally agreed that GP have significantly lower serum IgG concentrations (Klobasa et al., 1986, Ison et al., 2017, Craig et al., 2019b; 2019c) and serum immunocrit (Vallet et al., 2013, Vallet and Miles, 2017) than SP. Vallet et al. (2015) found that litter average immunocrit ratios on the first day of life increased from first (GP) to fourth parity progeny, which was reaffirmed in a more recent study (Vallet and Miles, 2017). Craig et al. (2019b) found higher serum IgG at 24 h in SP than GP despite the lack of differences observed in in vitro intestinal macromolecular permeability measurement (Wijesiriwardana et al., 2019). As recent studies have reported that primiparous and multiparous sows' colostrum has similar IgG concentrations and nutrient profiles at this time point, this suggests that SP ingest more colostrum than GP in this neonatal period, which has also been suggested by Ferrari et al. (2014). A reduction in IgG intake can reduce immunocompetence and hence survival rates since piglets rely on IgG as their primary immune defence until developing their own antibodies. This may help to explain the higher mortalities observed in GP compared to SP (Holyoake, 2006, Edwards et al., 2013, Craig et al., 2017a).

Passive immunity also encompasses IgM and IgA, maternal leucocytes, milk glycans, anti-inflammatory cytokines, and peptides that act to neutralise intestinal microbes (Pohl et al., 2015). Since passive immunity is derived solely from the dam, the immunocompetence of the dam is imperative. A lower immunocompetency of GP may not only contribute to the increased morbidity and mortality observed in GP but also reduce their growth performance by partitioning nutrients away from growth towards support of the immune system (Johnson, 2012).

Compromised acquisition of maternal immunity in GP could directly and indirectly affect their growth performance, health status, and survival to weaning and beyond. Not only could failure to mount an adequate humoral immune response result directly in morbidity or death of the piglet early in life when the acquisition of maternal humoral immunity (especially that of IgG) is paramount (Rooke and Bland, 2002), but these challenges may also have indirect effects on growth efficiency. For example, energy redirected to elicit an acquired immune response to a pathogen (or any associated innate inflammatory response) may be diverted from thermoregulation, growth of the musculoskeletal tissues, and (or) growth of the GIT, resulting in inefficient digestion of nutrients and a reduced ability to suckle effectively. Unfortunately, with the desire to breed from young gilts, this naivety in immunocompetence in the first parity is unavoidable. This enforces the need for good quarantine, biosecurity, and vaccination procedures to ensure increased productivity and health status of GP.

Long-term immune development in GP has not been extensively reported. However, studies using IUGR and LBW models suggest that GP may suffer from impaired or attenuated immune responses compared to their heavier and faster-growing SP counterparts later in life. This lack of appropriate immune response has been attributed to the reduced and (or) compromised intestinal growth and development. Dong et al. (2014) reported a reduced number of goblet cells and lymphocytes in intestinal epithelial cells in the small intestine of IUGR neonates along with reduced gene expression of cytokines, while D'Inca et al. (2010) saw a reduction in interleukin-6, a cytokine that contributes to host defence through the stimulation of acute phase responses, haematopoiesis and immune reactions. Furthermore, when these IUGR piglets failed to consume adequate colostrum and milk, lower circulating leucocyte and lymphocyte counts were observed (Hu et al., 2015). Compromised intestinal immune development of a light-for-age piglet (i.e. IUGR or LBW) can impact the ability of the piglet to amount an optimal immune response in the long term. This preweaning development of the immune response is imperative in preparation for the piglet for the intense intestinal changes it experiences at weaning.

High-stress events occurring during the piglet's early life, such as early weaning, mixing, or even inadequate milk intake, can cause improper intestinal immune development. While pigs are generally weaned more abruptly and early in commercial settings than in the wild, the slow growth and development of GP in commercial conditions arguably make them more immunologically underdeveloped than their SP counterparts at weaning. Given that early-weaned pigs exhibit impaired immunological responses to disease challenges compared to those weaned later (McLamb et al., 2013), it is unsurprising that a similar effect occurs in GP compared to their SP counterparts. Davis et al. (2006) reported lower concentrations of leucocytes of GP in response to Streptococcus suis infection, a disease that would usually raise leucocyte concentrations. Furthermore, Lessard et al. (2018) showed that piglets experiencing slower growth before weaning had reduced mucosal and systemic immune responses reflected by impaired cell proliferation of immune cell populations after weaning, reduced populations of antigen-presenting cells, and reduced B cells. Ultimately, it seems that while inflammation may increase after weaning in pigs with developed immunity, poorer development of the immune system in GP could result in attenuated immune responses, and this may partly explain poorer growth and higher postweaning mortalities (Craig et al., 2017a). Further work in the characterisation of immune responses in GP is required.

Gastrointestinal tract development in gilt progeny

The GIT plays an important role in metabolism, physiology, disease status and performance (Pluske et al., 2018), and examining differences in the growth and developmental processes between GP and SP may help to elucidate some of the underlying biological disparities observed. Unfortunately, literature on this is scarce. However, parallels can be drawn between GP and piglets of LBW or those that suffer from IUGR (Alvarenga et al., 2012). Early intestinal growth and development are primarily influenced by colostrum consumption in two ways. The first is through the uptake of colostral immunoglobulins and other proteins, electrolytes, and water, filling the intestinal enterocytes and increasing mucosal weights. The second is through colostral bioactive compounds including various types of growth factors such as epidermal growth factor, IGF-1 and IGF-2, and transforming growth factor-β (Xu et al., 2000; van Barneveld and Dunshea, 2011), and their ability to promote epithelial cell proliferation and maturation (Skrzypek et al., 2018). The activity of these growth factors is responsible for increases in tissue growth and functional changes (Widdowson and Crabb, 1976), increases in mucosal RNA content and protein content (Simmen et al., 1990), and increases in jejunal and ileal protein synthesis (Burrin et al., 1992). This ultimately results in increased intestinal mucosal weight and overall intestinal weight (Jensen et al., 2001; van Barneveld and Dunshea, 2011).

However, GP have lower total jejunal and ileal protein per g and lower small intestinal weight to length ratios compared to SP, suggesting that there is a reduction in the uptake of these proteins from colostrum (Craig et al., 2019b). This can negatively impact lifetime growth efficiency. Therefore, it is not surprising that LBW and IUGR piglets have been shown to have a longer, thinner intestine (D'Inca et al., 2010), similar to GP (Craig et al., 2019b). Furthermore, these piglets have a higher degree of intestinal injury, making the small intestinal barrier more susceptible to harmful pathogens in these animals (Everaert et al., 2017) compared to heavier-born piglets. In the same pigs from the Craig et al. (2019b) study, GP had higher permeability to larger molecules at weaning reflected in their lower transepithelial electrical resistance (Wijesiriwardana et al., 2019), which may be indicative of greater susceptibility to a 'leaky gut'.

Investigations into the intestinal microbiota of gilt progeny are limited but have recently gained traction due to the integral role that early microbiome development has on immune system development and function. Recent studies suggest that primiparous and multiparous sows have significantly different faecal microbiota 3 days postpartum, with differences observed between GP and SP at day 10 of lactation (Nowland et al., 2021). Furthermore, in a study by Gaukroger et al. (2021), primiparous and multiparous sows presented differences in faecal microbiota both prior to and after farrowing, with primiparous sows having an overall lower periparturient microbiota diversity. The reasons for these differences in microbiota between different parity sows are unclear, but presumably reflect different durations of exposure to commensal and pathogenic bacteria in the environment. Nevertheless, differences in the microbiome between primiparous and multiparous sows may also contribute to differences in subsequent growth performance and health status between GP and SP. Indeed, the parity differences in GIT microbiota in lactation may provide an avenue to develop on-farm approaches to improve GIT structure and function and performance of the sow that in turn may improve piglet performance (Nowland et al., 2021). However, further investigations into this area are required.

Conclusions

Gilt progeny are responsible for a significant loss of production due to their lower weights at birth, weaning and sale, and higher rates of mortality in comparison to SP. This is the consequence of numerous physiological factors which deserve to be further studied to understand how to best manage GP in commercial production. There is overwhelming evidence, both in the literature and anecdotally, that GP have inferior performance compared to SP, due to a myriad of interlinking factors relating to the anatomy, physiology, and behaviour of the primiparous sow and of the GP themselves. In this regard, there would be several key factors that may be responsible for the underperformance of GP including:

(1) Limited uterine capacity to support optimal growth of the litter ultimately resulting in degrees of IUGR;
(2) Low colostrum and milk production by the primiparous sow and therefore, reduced consumption by GP; and,
(3) Reduced growth and development of key organs such as the GIT and low immunocompetence in GP.

Collectively, these factors suggest that the poor performance of GP is a result of the inability of the primiparous sow to support her own growth concurrently with the growth of her litter. Therefore, it is recommended that selection and management strategies to improve GP performance should focus on:

(1) Selection for reproductive traits such as uterine capacity to improve birth weights of GP;
(2) Developing nutritional interventions that improve GP prenatal development and birth weights whilst also considering that gestating primiparous sows are likely to contribute additional energy to their own growth and maintenance requirements rather than foetal growth;
(3) Nutritional strategies to improve colostrum and milk yield in the primiparous sow thereby, supporting GP preweaning growth and improving their ability to copy with the stressors of weaning; and,
(4) Improving longevity and genetic gain reduces the need for replacement breeding stock, reducing the overall number of primiparous sows and their progeny in the herd.

Ethics approval

Not applicable.

Data and model availability statement

None of the data were deposited in an official repository. Data sharing is not applicable to this article as no new data were created or analysed.

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Declaration of interest

None.

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