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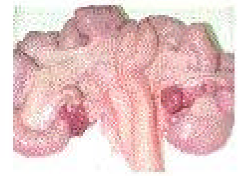

PARITY ASSOCIATED CHANGES IN REPRODUCTIVE PERFORMANCE: PHYSIOLOGICAL BASIS OR RECORD KEEPING ARTIFACT?

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Summary

Based on the retrospective analysis of sow herd production records it is evident that reproductive performance tends to increase gradually over the first three to four parities and then begins to decrease as sows reach parity seven or eight. Often, it has been assumed that this initial increase is related to the maturation of some components of the females' reproductive system. However, there is little published evidence of parity-based differences in reproductive processes such as estrus, ovulation, fertilization, and prenatal mortality. In addition, the confounding effects of parity (i.e. previous reproductive experience) and age are rarely separated in experiments. Retrospective comparison of the reproductive performance of groups of different parity females almost always ignores the fact that these groups are not comprised entirely of the same individuals. It is quite possible that reproductive performance increases over the first three to four parities because sub-fertile females are gradually removed from the herd. This article attempts to highlight differences in reproductive performance and physiology between gilts, primiparous, and multiparous sows and areas where parity-specific management might be used to increase reproductive efficiency.

Introduction

In swine production the term parity categorizes a sow or group of sows based on the number of litters farrowed. Parity is positively correlated with age but the two are not directly linked and differences in the rate that gilts reach puberty, as well as pregnancy failure in some gilts and sows followed by remating, results in considerable variation in the age of females with a specific parity category. The effects of age and parity are rarely separated in experiments reviewed (French et al., 1979) and it is important to recognize that in most studies it cannot be determined if the differences observed between parity groups were due to the aging process, the repeated reproductive cycles, or some combination of these two factors. While examples of parity-based differences in reproductive performance are numerous in the literature, evidence of physiological mechanisms that explain them are lacking. It is possible that physiological differences in the reproductive system of gilts and primiparous sows could be responsible for their decreased reproductive performance compared to multiparous sows. However, it is also quite possible that reproductive failure of sub-fertile gilts and primiparous sows eventually removes them form the breeding pool and in effect increases reproductive performance of the group in the subsequent parity.

Reproductive Performance

weaning-to-estrus interval

Parity 1, and to some extent parity 2 weaned sows, take longer to return to estrus than parity > 3

sows (Hurtgen et al., 1980; Clark et al, 1986; Koketsu and Dial, 1997). Parity 1 and 2 sows often consume less feed during lactation (Eisen et al., 2000) and exhibit a stronger relationship between lactation bodyweight loss and weaning-to-estrus interval compared to parity ≥ 3 sows (Table 1; Vesseur et al., 1994; Tantasuparuk et al., 2001). Decreased energy (feed) intake and increased energy demand for body growth and lactation result in a negative energy balance and a catabolic state in primiparous sows that inhibits LH secretion, maturation of follicles, and postweaning return to estrus. Sows that return to estrus 7 to 10 postweaning have a decreased farrowing rate and litter size compared to sows that return in ≤ 6 days (Steverink et al., 1999) and a greater percentage of parity 1 and 2 as compared to parity ≥ 3 sows return during this period of decreased subsequent fertility (Steverink et al., 1999; Koketsu, 1999; Tantasuparuk et al., 2001).

Table 1. Effect of parity and lactation weigh loss on weaning-to-estrus interval (WEI)

Weight Loss % *		**< 8%**	**8 – 15%**	**> 15%**
Parity	**No. Sows**	**WEI, d**	**WEI, d**	**WEI, d**
1	42	$8.9^{a\,x}$	$10.7^{ab\,x}$	$13.2^{b\,x}$
2	45	$6.5^{a\,xy}$	$7.0^{a\,y}$	$11.9^{b\,x}$
3	47	$5.6^{a\,xy}$	$6.7^{a\,y}$	$6.4^{a\,y}$
4	142	$6.1^{a\,y}$	$6.6^{a\,y}$	$6.5^{a\,y}$

* Lactation weight loss as a percentage of post-farrowing body weight
Means with different superscripts within a row ($^{a,\,b}$) and within a column ($^{x,\,y}$) differ $P < .05$
Adapted from Tantasuparuk et al., 2001

farrowing rate
The farrowing rate of gilts is typically about 10 to 15% lower than multiparous sows (Hurtgen and Leman, 1980; Clark et al., 1989). Primiparous sows also often have a 3 to 5% lower farrowing rate than multiparous sows (Hurtgen and Leman, 1980; Clark et al., 1989). Farrowing rate appears to remain relatively constant from parity 2 through 5 or more and then begins to decrease significantly around parity 8 (Clark et al., 1989). Mated primiparous sows that return to estrus and require a repeat breeding do not have a higher rate of recurrence of repeat breeding at parity 2 and 3 compared to parity 1 sows that do not require a repeat breeding (Elbers et al., 1996). In addition, litters that result from a repeat breeding tend to be larger (0.5 pigs) than litters from non-repeat breedings (Love, 1978; Tummaruk et al., 2001).

litter size
Litter size has a quadratic relationship with parity as it is smallest at parity 1, increases up to parity 4, 5, or 6 and then tends to plateau until it begins to decrease around parity 8 (Clark and Leman, 1986). A second parity "dip" in litter size was evident in several of the data sets reviewed by Clark and Leman (1986).

Reproductive Physiology

estrus and ovulation timing
The duration of standing estrus is often shorter in gilts compared to sows but the effect of sow parity on estrus and ovulation timing is largely due to differences in weaning-to-estrus interval between parity groups. A sow's weaning-to-estrus interval is inversely related to the duration of estrus and onset of estrus-to-ovulation interval she will exhibit in that sows that have short weaning-to-estrus intervals tend to have a long duration of estrus and a long onset of estrus-to-ovulation interval and vice versa (Soede and Kemp, 1997). Given that primiparous sows have

longer weaning-to-estrus intervals than multiparous sows, it is to be expected that they would have a shorter duration of estrus and onset of estrus-to-ovulation interval. However, even after correction for differences in weaning-to-estrus interval, Steverink (1999) reported a shorter duration of estrus for parity 1 and 2 compared to parity ≥ 3 sows (55 vs. 62 h; P < .001). Table 2 supports this finding since after correction for weaning-to-estrus interval differences, parity 1 sows tended to have a shorter duration of estrus and had a shorter onset of estrus-to-ovulation interval than parity ≥ 4 sows (52.3 vs. 54.6 h; P < .07 and 38.7 vs. 42.8 h; P < .002, respectively). Collectively, these data suggest that parity does have some affect on duration of estrus and onset of estrus-to-ovulation interval that is not related to weaning-to-estrus interval. Differences in weaning-to-estrus interval, duration of estrus, and onset of estrus-to-ovulation intervals between primiparous and multiparous sows may be large enough to have important implications for the AI protocols of parity-specific herds.

Table 2. Effect of parity on weaning-to-estrus interval (WEI), duration of estrus (DE), and onset of estrus-to-ovulation interval (EOI)

Sow Parity	**1**	**2**	**3**	**≥ 4**
No. Sows	98	86	102	208
WEI, d	05.1 ± 0.1 [a]	04.6 ± 0.1 [b]	04.4 ± 0.1 [bc]	04.3 ± 0.1 [c]
DE, h	51.5 ± 1.1 [a]	54.7 ± 1.2 [b]	57.0 ± 1.0 [b]	57.2 ± 0.7 [b]
EOI, h	38.2 ± 1.1 [a]	40.9 ± 1.1 [a]	42.1 ± 1.0 [b]	44.8 ± 0.7[c]
Corrected for WEI				
DE, h	52.3 ± 1.1	54.1 ± 1.1	54.7 ± 1.0	54.6 ± 0.8
EOI, h	38.7 ± 1.1 [a]	40.1 ± 1.1 [a]	40.0 ± 1.0 [a]	42.8 ± 0.8 [b]

Means with different superscripts ([a,b,c]) within a row differ P < .05
Belstra, Flowers, and See, unpublished data

ovulation and fertilization rate

Contradictory literature exists on whether ovulation rate increases with parity (Perry, 1954; Newman, 1963; Penny et al., 1971; Wrathall, 1971) or is independent of parity (Christenson, 1993; Tantasuparuk et al., 2001; Vonnahme et al., 2002). Ovulation rate tends to increases in gilts with each successive estrous cycle, especially in gilts that reach puberty at a young age (Kirkwood and Aherne, 1985). Sows do tend to have a greater ovulation rate than gilts, but it is not clear if ovulation rate increases over the first 4 to 6 parities as litter size does. There is some good evidence that age and not parity is the factor that influences ovulation rate (Christenson, 1993) and litter size (French et al., 1979). This may explain the contradictory findings in the studies mentioned above since age was not controlled.

When the percentage of ovulated oocytes fertilized (fertilization rate) in different parity sows inseminated within the same interval prior to ovulation was compared, one study suggested no difference between parities (Soede et al., 1995) and another found a small increase in fertilization rate in parity ≥ 3 compared to parity 1 and 2 sows (Steverink et al., 1997). Fertilization rate does not appear to be a major factor in the differences in reproductive performance between primiparous and multiparous sows. Insemination within 0 to 24 hours prior to ovulation provides high fertilization rates in gilts and sows (Kemp and Soede, 1997).

embryonic and fetal (prenatal) mortality

Given the increase in litter size observed over the first several parities, one would expect an increase in ovulation rate and prenatal survival or possibly just an increase in prenatal survival to account for this change. Based on extensive literature reviews (van der Lende and

Schoenmaker, 1990; Pope, 1994), the percentage of embryo mortality during the first 30 days of gestation, before uterine capacity becomes limiting, and the percentage of fetal mortality after 35 days of gestation, when uterine capacity can become limiting, does not seem to differ significantly between gilts and sows. Vonnahme et al. (2002) found that parity from 2 to 14 did not affect ovulation rate, number of viable conceptuses, or uterine horn length in sows from a commercial herd examined at 25, 36, and 44 days of gestation (Vonnahme et al., 2002). Such data may suggest that an increase in fetal survival (uterine capacity) is responsible for the increase in litter size as parity increases. However, no studies could be located that specifically investigated the effect of parity on embryo or fetal mortality.

Management and Environment

nutrition

Insufficient feed intake during lactation can reduce postweaning embryo survival (Hughes et al., 1984; Kirkwood et al., 1987a, b; Kirkwood et al., 1990; Baidoo et al., 1992; Zak et al., 1997). Increasing the protein and energy content of lactation diets to meet the increased needs and decreased feed intake of primiparous compared to multiparous sows is one way that parity-specific management might be able to improve reproductive performance.

High levels of pre- and postmating feed intake can affect ovulation rate and embryo survival, but they seem to have different effects in gilts, primiparous, and multiparous sows. High premating feeding levels can increase ovulation rate, but this so-called “flushing” effect has mainly been observed in developing gilts and often does not improve litter size (Dyck and Strain, 1979; den Hartog and van Kempen, 1980; Kirkwood et al., 1988). Aherne and Kirkwood (1985) concluded that flushing probably brings a low ovulation rate back to normal, rather than increasing ovulation rate above normal levels. Unfortunately, nutritional regimens that increase ovulation rate in gilts have also decreased embryo survival, particularly when continued postmating (review, den Hartog and van Kempen, 1980). This decrease in embryo survival may be partially due to the increased ovulation rate in flush fed gilts, however, there is also evidence that a high level of feed intake postmating reduces embryo survival by reducing postovulatory progesterone levels.

A number of studies demonstrated that a high feeding level during the first 10 to 15 days postmating decreases embryo survival in gilts (den Hartog and van Kempen, 1980; Dyck and Strain, 1983; Grandhi, 1988) and primiparous weaned sows (Jindal et al., 1996), but not in multiparous sows (Toplis et al., 1983; Dyck and Cole, 1986; Varley and Prime, 1993). Similarly, a high postmating plane of nutrition has also been associated with reduced circulating progesteroneconcentrations in gilts (Dyck et al., 1980) and primiparous weaned sows (Jindal et al., 1996), but not in multiparous sows (Varley and Prime, 1993) during early gestation. Several studies in gilts (Prime and Symonds, 1993), ewes, and cows suggest that this feed intake-induced reduction of peripheral progesteroneconcentration is the result of an increased metabolic clearance rate of progesterone due to increased hepatic blood flow and not increased activity of hepatic enzymes.

A positive relationship between circulating progesterone concentration 3 days post-estrus onset and embryo survival has been described in a number of studies utilizing the high postmating feed intake gilt model (Pharazyn et al., 1991a; Jindal et al., 1996, 1997; Mao and Foxcroft, 1998). Both Pharazyn et al. (1991a, b) and Jindal et al. (1997) observed a delayed postovulatory increase in progesterone(about 10 hours) in gilts on a high plane of nutrition post-estrus. Pharazyn et al. (1991a, b) hypothesized that postovulatory changes in progesteronemight be an important determinant of embryo survival, possibly by inducing changes in the oviductal environment or the rate of passage of the embryos. Further, the timing of changes in feed intake during the immediate post-estrus period seem to be critical in demonstrating an effect on embryo survival (Jindal et al., 1996; Pharazyn et al., 1991a, Foxcroft, 1997). This may suggest that there is a critical window of time during the postovulatory period where insufficient progesteronelevels can create embryo-uterine asynchrony and thus compromise subsequent embryo survival. There is certainly evidence to indicate that steroid levels affect uterine-embryo synchrony and thus survival through their actions on the oviductal (Mburu et al., 1998) and uterine environment (Roberts and Bazer, 1988).

Thus, a restricted feeding level near maintenance for 10 to 15 days postmating might be useful to increase embryo survival in gilts at least. However, a number of studies have failed to demonstrated reduced embryo survival in gilts fed at high levels postmating (Pharazyn et al., 1991a; Cassar et al., 1994; Liao and Veum, 1994; Dyck and Kennedy, 1995). In addition, food deprivation has been shown to alter steroid levelsand reduce embryo survival (Tsuma et al., 1996; Mburu et al., 1998). Therefore, it remains to be established if restricted feeding of gilts for 10 to 15 days postmating is necessary. High feeding levels are certainly advisable in weaned sows to improve body condition and reduced the interval to estrus (Allrich et al., 1979; den Hartog and van der Steen, 1981). Further, a high plane of nutrition during early pregnancy does not seem to reduce embryo survival in sows (Kirkwood et al., 1987b).

lactation length

Several studies have suggested that primiparous sows are more susceptible to the increased weaning-to-estrus interval and decreased farrowing rate associated with lactation lengths less than 21 days than their multiparous counterparts (Dial et al., 1995; Mabry et al., 1996; Koketsu and Dial, 1997; Le Cozler et al., 1997). For example, Mabry et al. (1996) found that sows could return to estrus and conceive efficiently at lactation lengths as short as 9 days for parity ≥ 3 sows, 12 days for parity 2 sows, and 19 days for parity 1 sows. Similarly, Koketsu and Dial (1997) suggested lactation lengths of 13 to 16 days for parity > 6 sows, 11 to 13 days for parity 2 to 6 sows, and 17 to 19 days for parity 1 sows as a guideline. Average lactation length currently seems to be around 18 days (PigCHAMP, 2002) and this means a range of 14 to 22 day lactations may be common for a group of weaned sows. Farms that wean more than one group (farrowing room) of sows per week could allow parity 1 and 2 sows, especially those that farrow late, a few extra days of lactation by weaning older parity sows from the next scheduled group in their place. This would help avoid subjecting parity 1 and 2 sows to short lactations although it would not be feasible on farms weaning once per week. Parity specific herds may have the advantage of being able to more easily adjust lactation length to meet the reproductive needs of the parity group(s) being managed.

It is interesting that several studies reported a decrease in litter size as lactation length decreased for parity ≥ 3 but not parity 1 and 2 sows (Walker et al., 1979; Clark and Leman, 1987; Koketsu and Dial, 1998). An injection of prostaglandin $F_{2\alpha}$within 24 to 48 h postpartum reduced this association between decreased litter size and short lactations in parity ≥ 3 sows (Koketsu and Dial, 2002). These data led to speculation that the reason litter size is not reduced following short lactation lengths in parity 1 and 2 as compared to parity ≥ 3 sows is because they may have a more rapid rate of uterine involution and postpartum prostaglandin $F_{2\alpha}$treatment might somehow improve this process in older parity ≥ 3 sows. Data on uterine involution in sows are scarce although in the cow, which has a different type of uterus and placentation than the sow, a slower rate of uterine involution has been associated with increasing parity (Zain et al., 1995). Even though parity 1 and 2 sows seem less susceptible to reduced litter size at lactation lengths < 19 days than parity ≥ 3 sows, they are more likely to exhibit extended weaning-to-estrus intervals and decreased farrowing rates than parity ≥ 3 sows. The decreased feed intake and increased metabolic demands placed on parity 1 and 2 compared to more mature parity ≥ 3 sows likely contribute to this phenomenon.

season

A seasonal decrease in sow fertility during the summer and early fall is a common and costly phenomenon in commercial swine production. Sows weaned from July to September take longer to return to estrus and more of them remain anestrus than at other times of the year (Claus and Weiler, 1985). Extra females (usually gilts) must be mated to meet farrowing targets since sows mated from July to September often exhibit a 10% decrease in farrowing rate and sometimes exhibit a 0.5 to 1.0-pig decrease in litter size compared to sows mated during the spring and winter (Love et al., 1993). A summer decrease in litter size should be interpreted cautiously since more gilt matings that produce smaller litters and more repeat breedings that tend to result in larger litters (Love, 1978; Tantasuparuk et al., 2000) occur during this period. In addition, culling policies are sometimes relaxed during the summer in order to meet breeding targets and mating old parity sows that should be culled may reduce herd reproductive performance.

The summer increase in weaning-to-estrus interval and decrease in farrowing rate are the most consistently observed characteristics of seasonal infertility. Primiparous sows exhibit a greater increase in weaning-to-estrus interval than multiparous sows during the summer period (Hurtgen et al., 1980; Clark et al., 1986; Xue et al., 1994). Lactation feed intake may be reduced during the summer months (Eisen et al., 2000) and primiparous compared to multiparous sows would be the most adversely affected by this since they have less body reserves and are still growing toward their mature size. Given the increased portion of primiparous compared to multiparous sows returning to estrus ≥ 7 days postweaning during the summer, it is surprising that Xue et al. (1994) found a decrease in total pigs born and born alive in multiparous but not primiparous sows during the summer in a retrospective record analysis of 42 herds. However, this finding is similar to reports that litter size is not reduced in parity 1 and 2 sows as it is in parity ≥ 3 sows following short lactation lengths (Walker et al., 1979; Clark and Leman, 1987; Koketsu and Dial, 1998).

Multiparous, primiparous, and nulliparous (gilts) sows mated from July to September all seem to exhibit a similar decrease in farrowing rate compared to the other three quarters of the year (Hurtgen and Leman, 1980). There is often an increase in irregular returns to estrus (> 24 days postmating) in sows mated during the period of seasonal infertility and it seems to be related to failure of some sows to respond to embryonic signals and complete maternal recognition of pregnancy (Love, 1978; Love et al., 1993). The fact that these types of failures result in complete rather than partial embryonic death may explain why a reduction of farrowing rate is more commonly observed than a reduction of litter size in sows mated from during the period of seasonal infertility.

Implications

Despite the fact that gilts and primiparous sows have significantly reduced reproductive performance compared to multiparous sows, there is little evidence of any substantial differences in the physiology of the reproductive process between these parity groups. This may be due to a lack of experiments designed to specifically examine the effects of age and parity on reproductive processes. Conversely, the increase in reproductive performance from gilt through the first few parities may be in part due to the removal of sub-fertile females from the breeding herd and not to some physiological change. Parity one and two sows have lower lactation feed intake, longer weaning-to-estrus intervals, an increased incidence of anestrus, and decreased farrowing rate and litter size compared to parity three or greater sows. Parity one and two sows are also more susceptible to increased weaning-to-estrus intervals and decreased farrowing rate than parity three or greater sows following short lactation lengths. Primiparous sows exhibit a greater increase in weaning-to-estrus intervals but a similar decrease in farrowing rate compared to multiparous sows during the period of seasonal infertility. High levels of postmating feed intake may exert differential effects on embryo survival in gilts and primiparous versus multiparous sows. Parity-specific insemination schedules may be beneficial given the longer weaning-to-estrus interval, shorter duration of estrus, and onset of estrus-to-ovulation interval of primiparous compared to multiparous sows.

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