Recent advances in pig reproduction: 2. Higher litter size

Recentes avanços na reprodução suina: 2. Leitegadas maiores

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Abstract

In the past 30 years, sows have been successfully selected for increased litter size. This review discusses the consequences of this selection for the reproductive physiology of sows, including the consequences for litter characteristics at birth. It also discusses breeding and management opportunities to deal with these modern genetics.

Keywords: Sow, litter size, genetic selection, management.

Introduction

As the economic success of sow husbandry relies very much – but not solely on the ability of sows to produce a high number of piglets per sow per year, breeding companies have, amongst others, selected for increased sow litter size.

Selection for higher litter size has resulted in a steady increase in sow litter size, which still continues. For example, in the Netherlands, sow litter size (total number born) has increased from 11.6 in 1996 to 13.3 in 2006 and 15.8 in 2016 (Kengetallenspiegel, Agrovision). However, concomitantly with this increase in total number born of about 0.2 piglets per year, the number of piglets born dead has also increased (from 0.7 to 1.2 piglets) and so did the percentage of piglets that died during lactation (from 11.5% to 14.3%). Similar trends are seen in Denmark between 1996 and 2011, where litter size increased from 11.2 to 14.8, but not in the UK where live born litter size only increased by 0.6 piglet to 11.4 in those 16 years (Rutherford et al., 2013).

In this review, we discuss aspects of selection for increased litter size. We first describe the consequences for sow fertility and piglet vitality, then we discuss potential physiological explanations and lastly, we discuss potential breeding and/or management solutions. This paper is largely based on Kemp et al. (2018).

Selection on Litter size

Consequences for fertility

A higher litter size is accompanied by a higher demand for milk from the suckling piglets. As feed intake is limited, this results in a higher sow weight loss during lactation, which can negatively affect subsequent pregnancy rate and litter size, especially in the first litter sow (see section above and for review e.g. Prunier et al. (2003).

Additionally, larger litters have on average lower piglet birth weights and more variation in piglet birth weight within litters (Quesnel et al., 2008). In organic sows, with a litter size of on average 17.4 ± 0.3 piglets, Wientjes et al. (2012) found that each extra piglet in the litter was related with a 40 g lower average birth weight, a 0.75% increase in the variation coefficient in birth weights within a litter and a 1.5 % increase in the percentage of piglets with a birth weight of less than 800 g.

Besides the negative phenotypic correlations, litter size is also genetically negatively correlated with birth weight (-0.30 to -0.49), and positively with variation in birth weight (0.21 to 0.25) and pre-wean mortality (0.25 to 0.45) (reviewed by Da Silva, 2018). Thus, to overcome this, breeding companies have to include those in their breeding goals.

Lower average and more variable piglet birth weights are an issue because of the increased chances of mortality of lower birth weight piglets, related with impaired energy reserves and thermoregulatory capacity, delayed and reduced colostrum intake and a disadvantage in competing with heavier littermates at the udder (Milligan et al., 2002; Damgaard et al., 2003; Quesnel et al., 2012). Moreover, lower average birth weight negatively affects growth performance and carcass quality of the piglets that survive (Beaulieu et al., 2010; Rehfeldt et al., 2008).

Physiological explanation: relation between litter size and (within-litter variation in) piglet birth weight

Litter size is determined by underlying physiological processes like ovulation rate, fertilisation rate of oocytes and embryo and foetal survival and development. Ovulation rates (as found in sow and gilt experiments all over the world in the last 36 years, reviewed by Da Silva (2018) have increased by approximately 0.2 ovulations per year, in sows as well as in gilts (see Figure 1).

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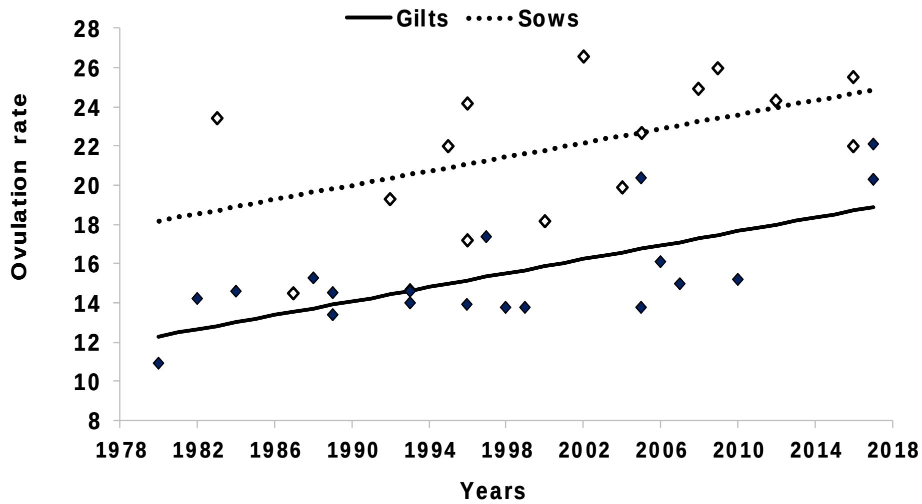

Figure 1. Ovulation rate as found in studies during the last 35 years, showing an increase of 0.2 ovulations per year in both gilts and sows (Da Silva, 2018).

Fertilisation rate is considered to be 90-100% when sows are inseminated at the right time with good quality semen (reviewed by (Kemp and Soede, 1997). Processes like ovulation rate and embryonic and foetal survival are related to each other and high ovulation rates and consequent uterine crowding may not only negatively affect embryo and foetal survival, but also placental development and thereby embryo and foetal development. This has been nicely demonstrated in experiments (e.g. by Père et al., 1997) in which Unilateral-Ovary-Hysterectomy (UHOX) was used to increase uterine crowding and ligation of one oviduct was used to decrease uterine crowding. That current high ovulation rates indeed affect embryo survival and embryo quality has recently been corroborated by (Da Silva et al., 2016; Da Silva et al., 2017) for sows and gilts, respectively. Figure 2 shows the increased gap between ovulation rate and number of embryos at day 35 of pregnancy with an increase in ovulation rate, in both sows and gilts. This increased gap is due to increased levels of early and late mortality. Moreover, in the gilts (Da Silva et al. 2017) high ovulation rates were related with higher within litter variation in weight (ß = 0.01). In sows, high ovulation rates were related with lower placental lengths, where each additional CL represented a decrease in placental length of 0.38 cm at day 35 of pregnancy (Da Silva et al. 2016).

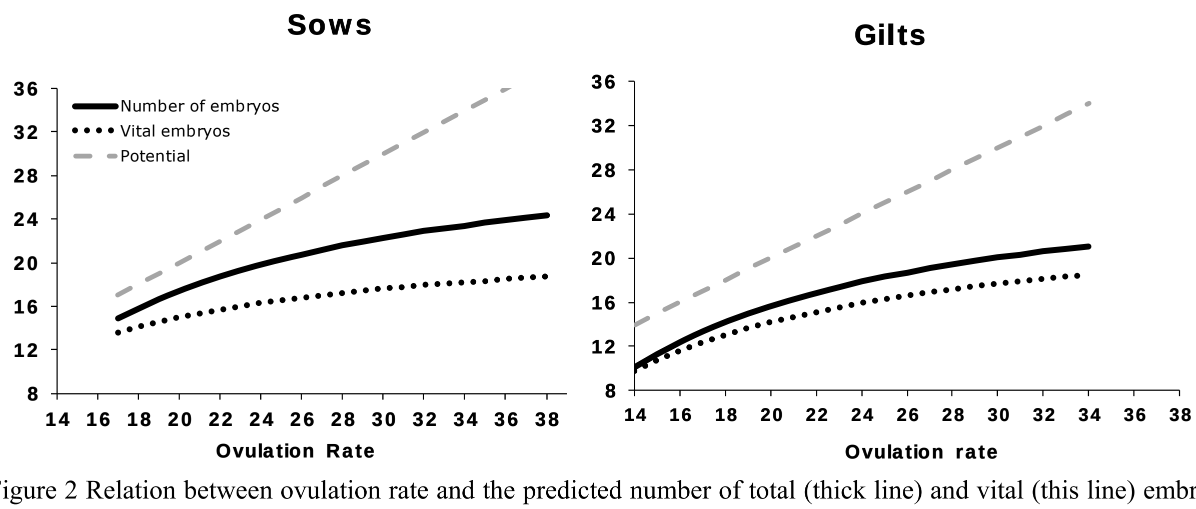

Figure 2 Relation between ovulation rate and the predicted number of total (thick line) and vital (this line) embryos at day 35 of pregnancy in sows and gilts. The dashed line (- - -) represents the potential number of embryos (i.e. ovulation rate) (Da Silva, 2017). Legend: The difference between total and vital embryos is considered to be late embryonic mortality and the difference between ovulation rate and total number of embryos is considered to be early mortality.

Da Silva et al. (2018) related estimated breeding values (EBVs) for litter size (TopigsNorsvin, Vught, The Netherlands) to ovarian and embryonic characteristics of gilts at day 35 of pregnancy (see Table 1). In these gilts, an increase in one unit of EBV for litter size (i.e. one piglet) was related with a 1.12 increase in ovulation rate, and no indications were found that embryonic or placental characteristics were negatively related with this EBV at this stage of pregnancy. Therefore, in these gilts, embryonic-placental units do not seem compromised at day 35 of pregnancy. It should be noted, however, that this group of gilts had a relatively high level of early embryo mortality, which may have negated potential negative effects of high ovulation rates on the embryonic-placental units.

Table 1. Significant relationships between estimated breeding values of gilts for total number of piglets born (EBV TNB), average piglet birth weight (EBV BW) and within litter piglet birth weight standard deviation (EBV BWSD) and ovarian and embryonic characteristics at 35 days of pregnancy (based on Da Silva et al., 2018).

	EBV TNB, n	EBV BW, Kg	EBV BWSD, g
Variable	beta	beta	beta
Ovulation rate, OR	1.12 ± 0.2	ns	ns
Corpus luteum weight, g	-0.11 ± 0.004	0.14 ± 0.04	0.0006 ± 0.0002
Total luteal mass, g	0.27 ± 0.12	ns	0.024 ± 0.01
Number of embryos	1.22 ± 0.4	ns	ns
Number of vital embryos	1.12 ± 0.3	ns	ns
Embryo weight	ns	ns	ns

ns - Non significant.

In the same study, Da Silva et al. (2018) analysed associations between EBVs for piglet birth weight and within litter variation in piglet birth weight with ovarian and embryonic characteristics at day 35 of pregnancy. The EBVs appeared not be related with ovulation rate; so, selection for a higher piglet birth weight and lower within-litter variation in piglet birth weight did not affect ovulation rate. Interestingly, both the EBV for piglet birth weight and for within-litter variation in piglet birth weight had a strong positive association with another ovarian characteristic; average corpus luteum (CL) weight at day 35 of pregnancy (see Table 1). In another study, Da Silva et al. (2017) used ultrasound to assess the average diameter of the 10 largest CL (5 per ovary) at day 20-30 of pregnancy and related that to subsequent piglet birth weight and standard deviation in piglet birth weight (see Figure 3). Each extra mm in CL diameter was related with an increase in average piglet birth weight of 36 g and a standard deviation in piglet birth weight of 24 g. Moreover, an increase in EBV for litter size was related to lower CL weights (Da Silva et al., 2018). Collectively, these data indicate that selection for litter size results in smaller CL during pregnancy, which is related to lower birth weights.

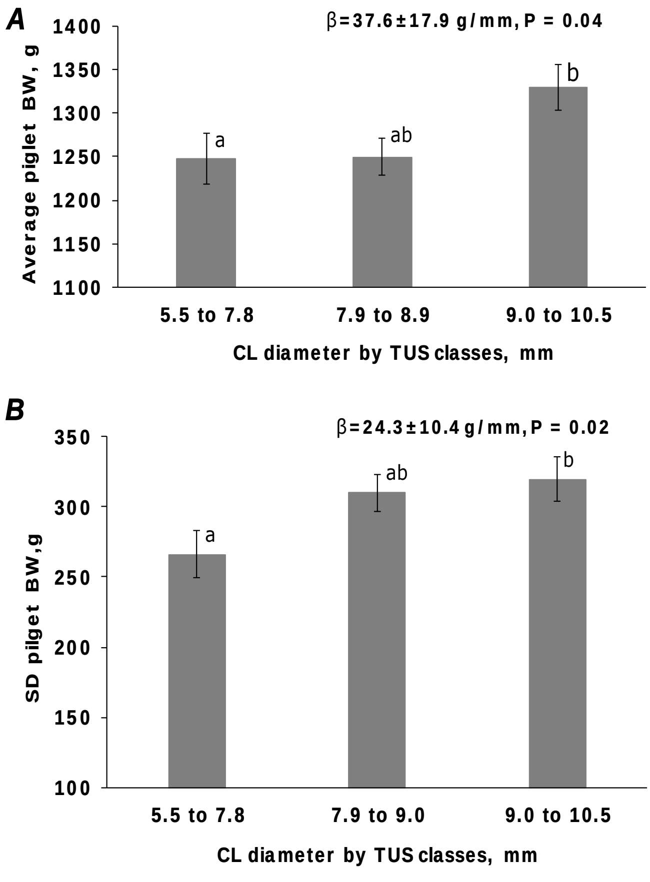

Figure 3 Effect of average CL diameter at ~ day 30 of pregnancy [5.5 to 7.8 mm (n = 23); 7.9 to 8.9 mm (n = 47); and 9.0 to 10.5 mm (n = 30)] on BW of total piglets born [P = 0.04; corrected for litter size class P < 0.0001] (panel A) standard deviation (SD) of BW of the total piglets born (P = 0.02) (panel B). [ab] P < 0.05. LSM ± SE (Da Silva et al., 2017).

What could be the physiological mechanism explaining the relation between CL weight and the litter characteristics? Average CL weight and variation in CL weight are positively correlated, so a higher average CL weight is accompanied by more variation in the CL pool. The CL pool originates from follicles that are recruited from the antral follicle pool at weaning (through the recruiting actions of the hypothalamus/pituitary system) and are selected to grow out to ovulatory sizes between weaning and oestrus. Considerable heterogeneity in size, morphology and hormone status of selected follicles has been reported in gilts during oestrus (Hunter and Wiesak, 1990; Knox, 2005). Heterogeneity in follicular (and oocyte) development at ovulation has been related with more variable early embryonic development and subsequent mortality of the less developed embryos (Pope et al., 1990; Xie et al., 1990). As larger follicles develop into larger CL (e.g. Wientjes et al., 2012), the positive relation between average CL weight during pregnancy and subsequent average piglet birth weight may therefore represent better developed follicles at ovulation that release higher quality oocytes (Marchal et al., 2002) that develop into better embryos. Indeed, at day 35 of pregnancy, a higher average CL weight was related with a higher vital embryo weight ($r = 0.17$) and a higher vital implantation length ($r = 0.24$) (Da Silva et al. 2018).

Thus, the association between CL size and piglet birth weight may arise from their common origin in the follicle development at ovulation. That this indeed might be the case is supported by studies in which glucogenic (insulin-stimulating) diets during lactation and/or the weaning-to-oestrus interval (Van den Brand et al., 2006; Van den Brand et al., 2009) and weight losses during lactation (Wientjes et al., 2013) affected subsequent piglet birth weight and within-litter birth weight variation.

To summarize, selection for higher litter size has resulted in more piglets with lower and more variable birth weights, related with compromised postnatal survival and performance of piglets. Two hypotheses have been explored to explain the relation between litter size and (variation in) piglet birth weight. (1) Foetal-placental units are compromised due to uterine crowding especially in sows with a high ovulation rate or (2) selection for litter size has resulted in a more variable pool of follicles at ovulation.

Breeding and management solutions

In breeding programmes, gilts are not selected for one trait (such as litter size) but for a number of traits that form the breeding goal. Based on the breeding goal, a selection index is created that uses multiple phenotypic traits that are important for the breeding goal (for example, birth weight and birth weight uniformity). Traits in the index receive a weight based on their economic value. Thus, potential negative effects of selection for litter size on (variation in) piglet birth weight or piglet survival are controlled by weighing these parameters (or correlated responses) in the selection index. Indeed, breeding companies have used piglet survival and/or (variation in) birth weight in their selection programs (reviewed by Zak et al. (2017).

As selection for litter size causes increased ovulation rate and uterine crowding, it would be of interest to further investigate the level of uterine crowding (i.e. compromised foetal- placental units) in relation to ovulation rate at different stages of pregnancy. It may also be of interest to consider selection on traits that improve uterine capacity (Freking et al., 2016). Such strategies might not result in improved within-litter birth weight when its cause lies more in the variable pool of follicles at ovulation than in available uterine space. Also, information from Genome-Wide-Association-Studies (GWAS) (Calus, 2010) in such studies could elucidate the genetic background of found relations.

From a management point of view, variation in birth weight can be partly counteracted by nutrition or management that prevents substantial weight loss during lactation (Wientjes et al., 2013) or affect follicular pool dynamics, e.g. glucogenic diets.

Concluding remarks

Selection for increased fertility, especially litter size, not only influences the reproductive physiology of the sow, but also has consequences for the welfare of both sows and piglets, as has been extensively reviewed (Rutherford et al., 2013; Baxter et al., 2013). Piglet vitality and welfare is affected by uterine crowding and sibling competition and by the management solutions to deal with these (e.g. cross-fostering). Sow welfare is affected both around parturition (pain during prolonged farrowing) and during lactation (udder damage and infection). These consequences have made increased litter size not only an important economic trait, but also an important issue of societal concern.

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