The Second Parity Sow

Causes and consequences of variation in reproductive performance

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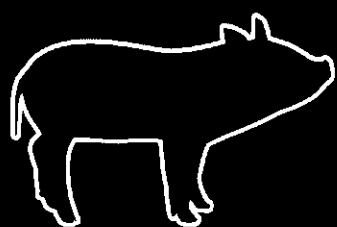
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Many sows show reduced litter sizes in their second parity compared with their first parity. The aim of the current thesis was to describe causes and consequences of variation in second parity reproductive performance and to evaluate if feeding strategies during early gestation affect reproductive performance and sow body weight recovery after first lactation. In a first study, effects of sow weight development from first insemination up to first weaning on second parity reproductive performance were studied. Weight gain from first insemination up to first weaning showed a positive effect on non-pregnancy as well as on litter size, especially on a farm where gilts were relatively young and light at time of first insemination. In a second study, effects of weight loss during lactation were evaluated on embryonic survival and metabolic parameters during lactation and gestation in primiparous sows that were fed close to ad libitum. Sows with a high (>13.8%) weight loss showed a lower embryonic survival and fewer vital embryos at day 35 of gestation compared with sows with a lower weight loss, whilst no differences in metabolic parameters (IGF-1, NEFA, urea) were seen. The fact that the number of implantation sites was lower in high weight loss sows compared with low weight loss sows indicates that the negative effects of weight loss were already present during late lactation or early gestation. In a third study, a data-analysis using 46,500 sows was performed to assess relations between second parity performance and reproductive performance in later parities. Results showed that farrowing rate and litter size in parity 3 and up, as well as parity at culling, were related to second parity reproductive performance. These relations with second parity litter size were affected by first parity litter size. In practice, feed allowance during early gestation is often limited and might not be sufficient to support growth and recovery from lactation. The question was therefore raised if increased feed or protein intake during early gestation could improve litter size. In two experiments, the effects of an altered feeding strategy during the first month of gestation on farrowing rate and litter size (exp. 1) and embryonic survival and embryonic and placental development and metabolic parameters (exp. 2) were assessed. In Experiment 1, a 30% higher feeding level increased litter size with two piglets, without negatively affecting piglet birth weight. In Experiment 2, designed to find a physiological explanation for these results, an increased feeding level did not affect embryonic survival, embryonic development or placental development. Furthermore, no relations with metabolic parameters were found. From this thesis it can be concluded that second parity reproductive performance is related to reproductive performance in later parities. In order to improve second parity reproductive performance, weight loss during first lactation should be limited and gilts should be heavier at first weaning than at first insemination. Further, increased feeding levels during early gestation improve sow body weight recovery, without negatively affecting reproductive performance.
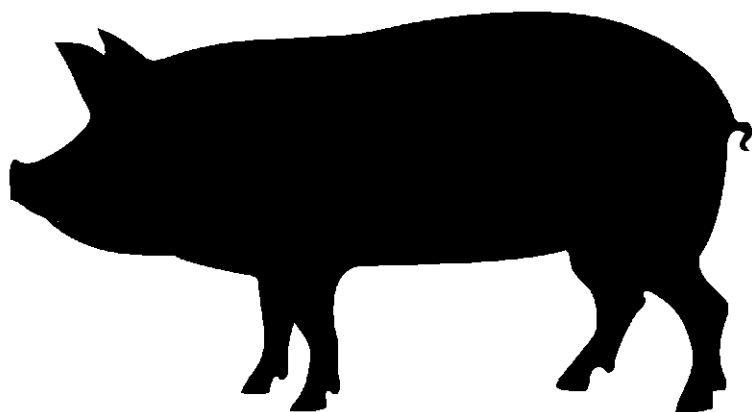
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Chapter 1

General Introduction

Around 19% of the reproductive sows in a herd are second parity sows, i.e sows after first weaning. Their reproductive performance, i.e. farrowing rate and litter size, therefore has a large impact on farm productivity. In general, reproductive performance is supposed to increase with increasing parity, reaching the highest level from parity 3 to 5 (Koketsu et al., 1999; Hughes and Varley, 2003). Many sows, however, show an equal or lower litter size in second parity than in first parity (Morrow et al., 1992; Saito et al., 2010), which negatively influences reproductive efficiency of second parity sows and thereby farm productivity (Willis et al., 2003). Since reproductive failure is one of the main reasons for culling in young sows (Lucia et al., 2000), improving second parity reproductive performance might also increase sow longevity and thereby decrease replacement costs. Furthermore, second parity reproductive performance might also be related to subsequent reproductive performance, however, little information is available on this relation.

Suboptimal litter sizes or farrowing rates in second parity sows are often related to (excessive) weight loss during first lactation (Thaker and Bilkei, 2005; Schenkel et al., 2010). Since litter sizes and number of piglets weaned have increased in the last decade (Figure 1.1), the metabolic demands on first litter sows have also increased, whilst feed intake did not. This can result in more weight loss. Furthermore, selection on short weaning to oestrus interval (WOI) has been successful and most sows come in oestrus 4-5 days after weaning. This period, however, might not be sufficient for sows to recover from high lactation weight losses. Both the higher weight loss and short WOI can negatively influence follicle and oocyte development and/or embryonic survival and make sows more at risk for reduced litter sizes or farrowing rates in second parity.
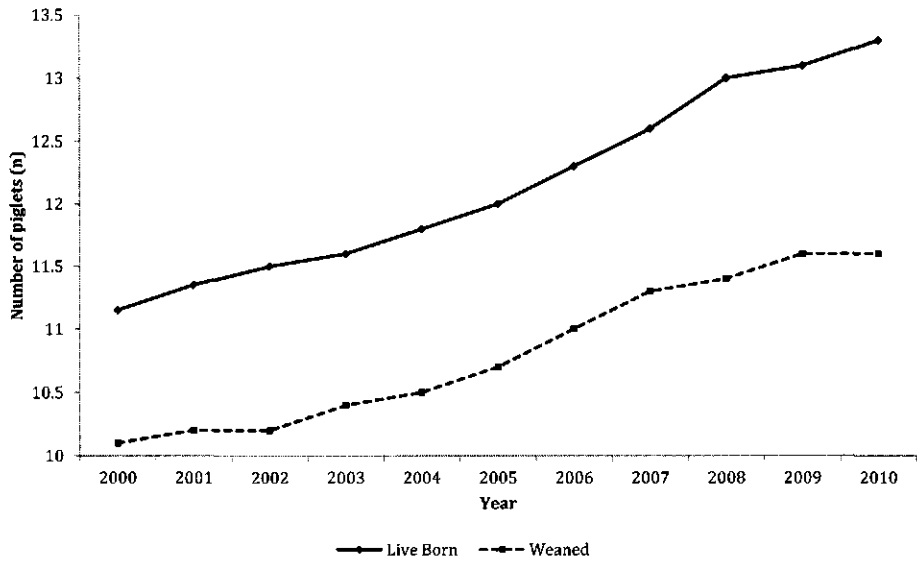

Figure 1.1 Phenotypic trend of number of piglets born alive and number of piglets weaned in the Dutch pig husbandry in the past decade (Agrovision BV, Deventer, The Netherlands).

1.1 Lactation: Weight loss and effects on reproductive functioning

During lactation, sows need energy and nutrients for maintenance and growth, but the highest energy demand is for milk production. Feed intake during lactation is often not sufficient to cover these energetic demands for milk production, maintenance and growth (Prunier et al., 2010; Bergsma, 2011). Energy for maintenance has been estimated to be 0.44 MJ/kg $BW^{0.75}$ (Everts and Dekker, 1994). Energy for milk production is often measured as energy needed for 1 kg of piglet growth. Producing one kg of piglet costs about 3.8 kg of milk (~25.5 MJ ME of feed). This means that a 200 kg sow, weaning 11.7 piglets with a litter growth of 2.9 kg/day (standard sow in feeding manual, TOPIGS, Vught, The Netherlands) should ingest about 100 MJ ME which is equal to 7.8 kg feed containing 12.8 MJ ME/kg. In practise feed allowance is often calculated based on the assumption that the daily energetic demands of sows are 1% of body weight for maintenance and 0.5 kg of feed per piglet (NRC recommendation). For a 200 kg sows weaning 11.7 piglets this means a feed intake of 7.8 kg. However, average feed intake rarely exceeds 6 to 7 kg per day (Eissen et al., 2003; Kruse et al., 2011). First litter sows might even eat less than 6 kg per day (Bergsma, 2011), since their feed intake is estimated to be about 15% lower than multiparous sows (Koketsu et al., 1996a).

When feed intake is not sufficient to fulfil the energy demands, sows use body reserves, i.e. body protein and body fat, as an alternative energy source to ensure continuous milk production (McNamara and Pettigrew, 2002) and coverage of maintenance costs. Even though some weight loss is acceptable, high body reserve losses, e.g. more than 10-12% weight loss or more than 10% protein loss, have been reported to negatively affect weaning to insemination interval, ovulation rate and follicle and oocyte quality (Zak et al., 1997b; Clowes et al., 2003a; Vinsky et al., 2006). First litter sows are considered to be especially sensitive for negative effects of body reserve losses, since they are physically immature at first farrowing and thus only have limited body reserves and still need energy for growth and further development.

Up to the mid-nineties, negative effects of severe feed and protein restriction during lactation were mainly expressed as a prolonged weaning-to-oestrus interval (WOI), while more recent studies mainly show negative effects on ovulation rate and embryonic survival (Table 1.1). The shift from prolonged WOI to reduced embryonic survival and ovulation rate is probably due to genetic selection for a short WOI (Quesnel, 2009). When sows with (a high) lactation weight loss return to oestrus shortly after weaning, follicle and oocyte quality can be compromised since the follicles developed during a period of negative energy balance (reviewed by Quesnel (2009)) and are recruited immediately after weaning. If WOI is substantially prolonged, follicles and oocytes develop during a period of positive energy balance, which benefits their quality. Compromised follicle development can lead to lower quality oocytes (Pope et al., 1990) and less developed corpora lutea (CL).

Whilst low quality oocytes can lead to low quality embryos, increased embryonic losses (Zak et al., 1997a) and eventually to lower litter sizes and farrowing rates.

1.1.1 Physiological background of lactational influences on follicular growth and development
Follicular growth is influenced by Follicle Stimulating Hormone (FSH, small follicles up to 4 mm) and Luteinising Hormone (LH, mainly follicles >4 mm). During the first weeks of lactation, antral follicle development is minimal due to the inhibition of pulsatile LH release. The inhibition of LH release is caused by the suckling stimuli of piglets, which results in the release of endogenous opoids that inhibit gonadotrophin-releasing hormone (GnRH) release from the hypothalamus (De Rensis et al., 1993; Quesnel and Prunier, 1995).

Table 1.1 Effects of high or low lactation feed or protein intake on weaning to oestrus interval, ovulation rate and embryonic survival (adapted from Quesnel (2009)

Reference	Parity	WOI (days)		Ovulation Rate		Embryo Survival	
Feed intake		High[#]	Low[§]	High[#]	Low[§]	High[#]	Low[§]
King and Williams (1984a)	1	10.8[b]	23.0[a]	14.4	13.5	70	72
King and Williams (1984b)		14.2[b]	17.9[a]	12.3	12.6	62	61
Kirkwood et al. (1987)	2	4.3[b]	5.8[a]	18.2	18.7	83[a]	68[b]
Kirkwood et al. (1990)	2	6.9[b]	8.9[a]	17.6	17.7	79[a]	72[b]
Baidoo et al. (1992a)	2	5.9[b]	7.3[a]	16.4	17.2	81[a]	67[b]
Zak et al. (1997a)	1	3.6[b]	5.0[a]	19.9[a]	15.4[b]	88[a]	64[b]
Zak et al. (1998)	1	4.2[b]	6.3[a]	14.4	15.6	83	72
Van den Brand et al. (2000b)	1	5.1	5.7	18.2[a]	16.2[b]	88a	64[b]
Vinsky et al. (2006)	1	5.3	5.4	18.3	18.2	79[a]	68[b]
Protein intake							
Mejia-Guadarrama et al. (2002)	1	5.4	5.3	23.4[a]	20[b]	72	73

[#] High ~ ad libitum; [§] Low ~50% ad libitum; [a,b] significant difference between High and Low

As lactation progresses, LH pulsatility is partly restored, which allows follicles to develop up to 2-5 mm at weaning (Lucy et al., 2001). In addition, LH stores in the pituitary increase during lactation, as is shown by a greater LH release in response to injection with oestradiol bezoate (Elsaesser and Parvizi, 1980; Kirkwood et al., 1984). FSH concentrations are less influenced by factors related to lactation, but more so by ovarian factors (Quesnel and Prunier, 1995).

After weaning, LH pulsatility changes from low frequency, high amplitude to a high frequency, low amplitude pattern which stimulates follicles to develop to pre-ovulatory size about 3-4 days later (~ 7-8 mm; Soede et al. (1998)). If LH pulsatility is not restored during the course of lactation, follicle development at weaning will be impaired and follicular growth up to the pre-ovulatory stages will take longer, increasing the weaning to oestrus interval (Lucy et al., 2001). The restoration of LH pulsatility, and thus follicle development, during and after lactation may be related to the reduced intensity of the suckling stimuli, but can also be affected by the nutritional state of the sow (Quesnel and Prunier, 1995; Figure 1.2), as will be described below. Besides by influencing LH pulsatility, the nutritional or metabolic state of the sow can also directly influence follicle development and oocyte quality.

The effect of the metabolic state of the sow on LH release and follicle and oocyte development are mediated by metabolic hormones and metabolites, such as insulin, Insulin-like-Growth Factor-1 (IGF-1), glucose, leptin and Non Esterified Fatty Acids (NEFA) (Webb et al., 2007, Figure 1.2). Insulin and IGF-1 concentration are low during feed or protein restriction (Baidoo et al., 1992b; Van Den Brand et al., 2001b; Mejia-Guadarrama et al., 2002). Insulin has been reported to stimulate follicle and oocyte development both indirectly, by stimulating LH secretion in hourly fed sows (Koketsu et al., 1996b), and directly on the ovarian level (Quesnel et al., 2007). Furthermore, insulin seems to stimulate IGF-1 concentrations during periods of negative energy balance (Van Den Brand et al., 2001b). Under anabolic conditions, IGF-1 concentration is increased in response to an increasing Growth Hormone (GH) concentration. During lactation, GH concentration is often high whilst IGF-1 concentration is low (Kraetzl et al., 1998; reviewed by Quesnel, 2009). This indicates an uncoupling of the link between GH and IGF-1 and during this uncoupling insulin can stimulate IGF-1. In pigs, IGF-1 is one of the most intensively studied metabolic hormones related to follicular development. IGF-1 concentrations can influence follicle development either indirectly, by acting on the hypothalamus and thereby influencing pulsatile LH release by the pituitary (Quesnel and Prunier, 1998; Van Den Brand et al., 2001b) or directly by increasing the ovarian response to gonadotropins (reviewed by Quesnel, 2009). During lactation, the mammary gland uses glucose for milk synthesis which results in low circulating glucose levels. Low glucose concentration might influence LH release from the pituitary, since glucose has been reported to positively affect LH release from the pituitary (reviewed by Barb et al., 2001). Leptin concentrations are positively related to body fatness of sows (Estienne et al., 2000) and results from in-vitro studies indicate that leptin can affect GnRH release and thereby LH secretion (reviewed by Barb et al., 2008). In in-vivo studies in pigs, however, the relation between leptin and subsequent reproductive performance is less clear (De Rensis et al., 2005; Summer et al., 2009). NEFA concentrations are high during lactation and are indicative for fat mobilization (Hultén et al., 2002a; Valros et al., 2003). In dairy cattle, high NEFA concentration have been related to reduced embryonic survival, either by negative effects on follicle and oocyte development or by affecting the uterine environment (Leroy et al., 2008; van Hoeck et al., 2011). In pigs, it's relation with follicle and oocyte development is, however, not clear.

In conclusion, feed or protein restriction during lactation influences the metabolic state of sows and can thereby affect reproductive performance in subsequent parities. Most of this information, however, is based on studies in which severe protein and/or feed restriction is applied (Table 1.1). In practise, sows are often fed (close to) ad libitum and variations in weight loss during lactation is a balance between voluntary feed intake, milk production and costs for maintenance. Though also under these circumstances weight loss has also been related to reduced reproductive performance. However, effects of weight loss under practical circumstances on underlying traits, such as ovulation rate, embryonic survival and metabolic parameters, have hardly been studied.
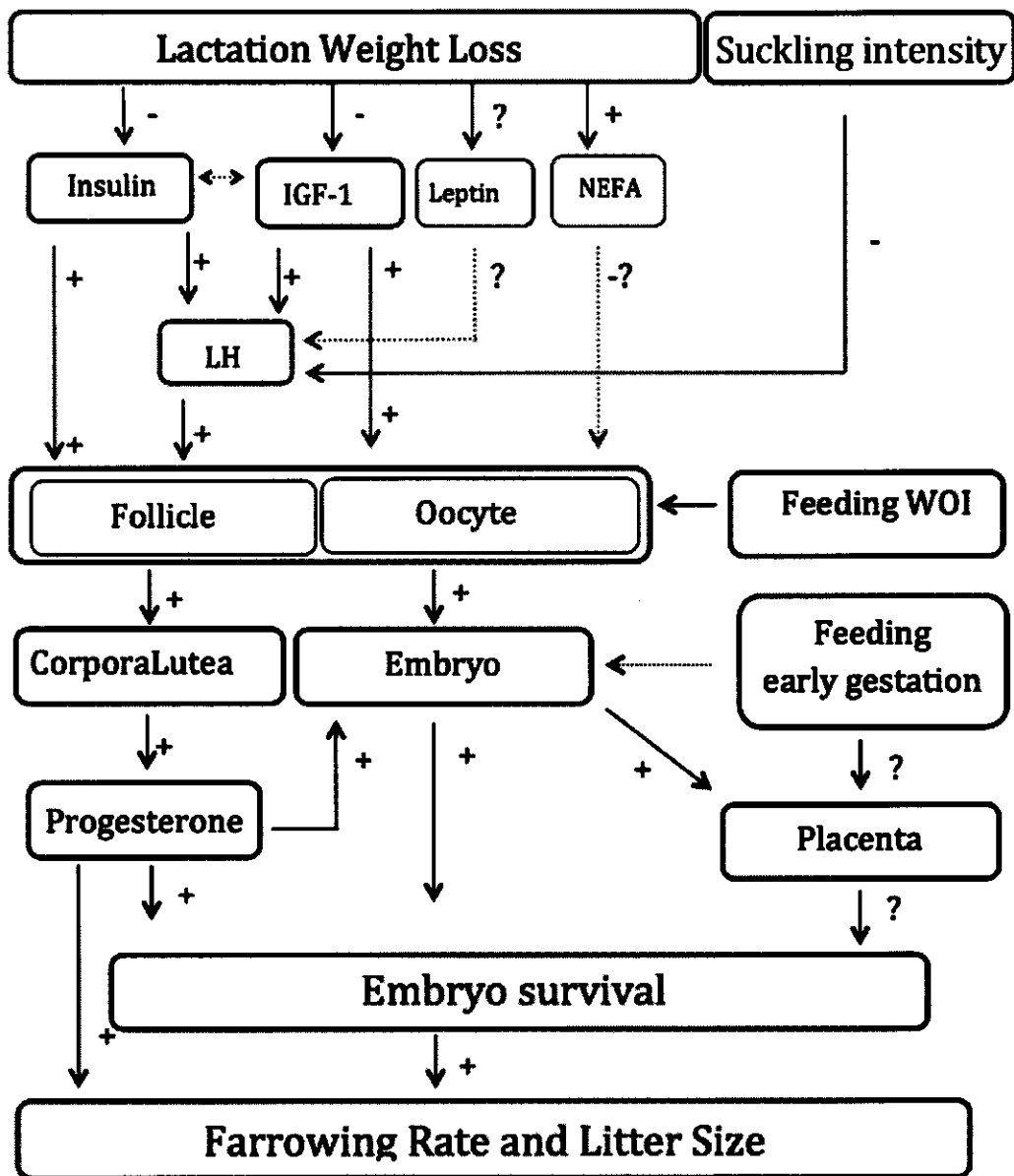
Figure 1.2 Schematic overview of relations between weight loss and reproductive
and metabolic hormones and their relation with reproductive measurements.

1.2 Weaning to oestrus interval and early gestation: reproduction and sow development

After weaning, when adequate feeding levels are provided, sows quickly return to an anabolic state (Kraetzl et al., 1998). During the weaning to oestrus interval, sows are often fed a fairly high amount of a high energetic diet, which is called 'flushing'. Flushing stimulates plasma concentrations of insulin and IGF-1 (Cox et al., 1987), which stimulates follicle development. Around 4 to 5 days after weaning, most sows come into oestrus and can be inseminated. Ovulation takes place at about two-thirds of the oestrus (Soede et al., 1994). After ovulation, oocytes are released into the oviduct and follicles develop into CL. Fertilized oocytes develop into embryos, whilst CL produce progesterone throughout gestation, which is important for the maintenance of pregnancy. If CL regress and progesterone concentrations decrease, pregnancy is terminated. Progesterone also affects (synchronous) development of the fertilized oocytes and the uterine environment, which is necessary for successful implantation around day 12 of gestation. A low follicle quality, caused by weight loss during lactation, can result in CL that produce less progesterone, which reduces progesterone concentrations during (early) gestation.

Furthermore, less developed follicles might also decrease luteal weight. Luteal weight, in turn, is related to progesterone concentrations and a reduced luteal weight might decrease progesterone concentrations. Reduced progesterone concentration, in turn, can cause asynchronous development of embryos and the uterine lumen and therefore decrease embryonic survival (Pope, 1988; Ashworth, 1991), which can lead to a lower litter size and perhaps a lower farrowing rate at term.

Even though sows are fed a high energetic diet during the WOI, the 4 to 5 day period is too short for sows to fully recover from weight loss during lactation and restoration of body reserves is therefore needed during gestation. The recovery period is especially important for young sows, since they also need to grow to reach their mature body size, which is reached around their third or fourth parity (Everts, 1994). During the first two-thirds of gestation, the energetic demands for litter growth are low and young sows can use this period to recover from lactation (Dourmad et al., 1996). In practise, however, feeding levels during early gestation are often low. The low feeding levels are based on studies in gilts which report a reduced embryonic survival when gilts are fed a high feeding level during early gestation (Jindal et al., 1996; De et al., 2009). This reduced embryonic survival has been related to a decreased systemic progesterone concentration (Jindal et al., 1996), caused by an increased clearance of progesterone in the liver in gilts on a high feeding level (Prime and Symonds, 1993). Results from studies on the effects of a high feeding level on progesterone concentrations and reproductive performance in multiparous sows, however, are inconclusive (Kirkwood et al., 1990; Varley and Prime, 1993; Virolainen et al., 2005b). Studies on the effect of feeding level during early second gestation on reproductive performance in second parity sows are to our knowledge not

reported. If high feeding levels during early pregnancy do not negatively affect reproduction in second parity sows, feeding levels during early pregnancy can be increased, which improves sow body recovery and growth to maturity. Furthermore, a higher feeding level during early gestation might even improve subsequent reproductive performance, as has been reported for multiparous sows by Sørensen and Thorup (2003).
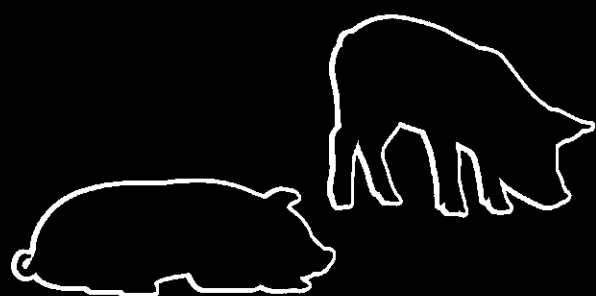
1.3 Aim and outline of the thesis

Many sows show a suboptimal second litter size compared with their first litter size. This has mostly been related to negative effects of weight loss during first lactation. The aim of this thesis was to describe causes of variation in second parity litter size and farrowing rate, to study relations between second parity reproductive performance and subsequent reproductive performance and to evaluate if feed strategies during early gestation affect reproductive performance and body weight recovery after lactation in second parity sows.

First parity sows are especially sensitive for lactation losses since they do not have enough body reserves at first farrowing and have a limited feed intake capacity. Many studies have shown that (severe) feed or protein restriction, as a model for weight loss, during first lactation affects reproduction in second parity. In practise, however, sows are often fed (close to) ad libitum and variations in lactation weight loss are mainly due to variation in voluntary feed intake, milk production and maintenance costs. Effects of weight loss on reproductive functioning and metabolism might therefore be different during severe feed restriction than when feeding levels are close to ad libitum. Furthermore, the effects of weight loss on reproductive functioning are often assessed at the embryonic stage and information on farrowing rate and litter size is scarce. More information on the effects of the different sow (weight) development parameters on farrowing rates and litter size in second parity can optimize farm management of gilts and first litter sows up to first weaning. **Chapter 2** therefore describes the association of farrowing rate and litter size in second parity with body weight development in first parity sows under practical circumstances. Many studies only follow metabolic changes during lactation up to the WOI, whilst metabolic differences present during lactation might be continued into (early) gestation and thereby influence embryonic survival. **Chapter 3**, describes the associations of weight loss during lactation with reproductive performance on day 35 of second gestation. In addition, associations with metabolic profiles during the ast 10 days of lactation and during the first month of second gestation are described, using first parity sows which were fed a lactation feeding regime commonly used in practice. Around 50% of the second parity sows show a lower litter size in second compared with first parity. The reduced reproduction decreases reproductive efficiency of second parity sows but might also lead to earlier culling. It is, however, not known if second parity reproductive performance is also related to reproductive performance in later parities. For farm profitability it is important to know if such an relationship exists. In **Chapter 4**, using a large dataset, the relations of failure to farrow

and litter size in second parity with reproductive performance in later parities are investigated. Furthermore, Chapter 4 also discusses relations between litter size in first parity with litter size in second parity and their combined effect on litter size in subsequent parities.

Lactation is a large burden for sow body condition, especially for first parity sows that are physically immature and have relatively low body reserves at time of first farrowing. An increased feeding level in early second gestation can help young sows to recover from lactation losses. However, in practise, feeding levels during early gestation are often low. The low feeding levels are based on studies in gilts, which report a reduced embryonic survival when using high feeding level during early gestation. Little information is available on the effects of feeding level during early gestation on reproductive performance in second parity sows. A higher feeding level during early gestation might even improve reproductive performance in second parity sows, as has been described for multiparous sows. **Chapter 5** therefore studies if an increased feed and protein level during the first 4 weeks of second or third gestation improves sow recovery from lactation losses and if it improves litter size and farrowing rate. Based on results from Chapter 5, **Chapter 6** investigates the possible physiological mechanisms involved, by studying hormonal and metabolic alterations and their relation with reproductive performance during the first 35 days of second gestation.

In the last chapter of this thesis, **Chapter 7**, the findings from Chapters 2 to 6 are combined and discussed and practical recommendations will be given.

Chapter 2

Effect of live weight development and reproduction in first parity on reproductive performance of second parity sows

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Effect of live weight development and reproduction in first parity on reproductive performance of second parity sows

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ABSTRACT

An impaired reproductive performance in second parity compared to first parity sows, decreases reproductive efficiency and, perhaps, longevity of sows. This study aims to quantify the effect of live weight development and reproduction in first parity on reproductive performance of second parity sows, i.e. pregnancy rate as well as litter size. Measures of sow development (live weight at first insemination, farrowing and weaning) and reproduction (total number of piglets born, weaning to insemination interval, lactation period, number piglets weaned) were recorded on two experimental farms. Logistic regression analysis was done for the binary outcome 'non-pregnancy from first insemination after first weaning' (yes/no). General linear regression analysis was used for litter size from 1st insemination in second parity. Repeat breeders were omitted from the analysis on litter size in second parity, since a prolonged period between weaning and conception can positively influence litter size. Farms differed significantly in measures of sow live weight development and therefore data were analyzed per farm. Compared with gilts from farm A, gilts from farm B were older and heavier at: first insemination (275 ± 0.9 days and 145 ± 0.8 kg for farm B vs. 230 ± 0.6 days and 124 ± 0.5 kg for farm A), first farrowing (resp. 189 ± 1.1 vs. 181 ± 0.9 kg) and first weaning (resp. 165 ± 1.1 vs. 156 ± 0.9 kg). Weight loss during lactation was similar for both farms (resp. 24.9 ± 0.7 and 23.7 ± 1.0 kg). Gilts from farm A, however, gained more weight in the period between first insemination and first weaning compared with gilts from farm B (resp. 36.1 ± 0.8 and 20.9 ± 1.3 kg). Non-pregnancy in second parity was 11% for farm A and 15% for farm B. Litter sizes in first and second parity were, respectively, 10.7 ± 0.1 and 11.6 ± 0.2 for farm A and 11.8 ± 0.1 and 11.6 ± 0.1 for farm B. Variables associated with non-pregnancy and litter size in second parity differed between farms. On farm A, mainly sow live weight development was associated with non-pregnancy and litter size in second parity, whilst on farm B variables like total number born in 1st parity and sow line, were associated with non-pregnancy and litter size in second parity. On both farms, higher weight gain from first insemination to first weaning was associated with a decrease in non-pregnancy (odds ratio 0.7 per 10 kg for farm A and 0.8 per 10 kg for farm B) and on farm A with higher litter size in second parity ($\beta = 0.42$ per 10 kg weight gain). Results show that sow live weight development affects reproductive performance in second parity, especially on farm A where gilts are relatively light or young at first insemination. Management of these animals should aim to optimize development at first insemination and to increase growth between first insemination and first weaning in order to optimize production in second parity.

Key Words: Litter Size, Pregnancy Rate, Reproductive Performance, Sows, Second Parity

1. INTRODUCTION

Reproductive performance, i.e. farrowing rate and litter size, is supposed to increase as parity increases, reaching the highest levels from parity 3 to 5 (Koketsu et al., 1999; Hughes and Varley, 2003). Second parity sows, however, often have lower pregnancy rates and/or smaller litter sizes from first insemination compared with first parity sows (Morrow et al., 1989). This phenomenon is called second litter syndrome (SLS). SLS decreases reproductive efficiency of second parity sows and might decrease sow longevity, as reproductive failure is the main reason for culling in young sows (Zak et al., 1997b; Lucia et al., 2000). Genetically there is a high correlation between litter size in parities 1 and 2 (0.88; Holm et al., 2005) and (0.83; Hanenberg et al., 2001), however phenotypic correlation is low (0.04; Hanenberg et al., 2001), indicating a high environmental influence on litter size.

Severe body reserve depletion during lactation is a well-known factor associated with reproductive failure in sows (Prunier et al., 2003). Effects of metabolic status on subsequent reproductive functioning have been extensively studied. Feed restriction as well as protein restriction during lactation, and therefore an increased negative energy balance, have been reported to decrease follicular development (Quesnel et al., 1998; Clowes et al., 2003a), to increase weaning to estrous interval (Zak et al., 1997a), to decrease ovulation rate (Zak et al., 1997a; Vinsky et al., 2006), and to decrease embryonic survival (Vinsky et al., 2006) and litter size (Revell et al., 1998; Prunier et al., 2003). In these studies sows are usually slaughtered during early pregnancy and effects on farm variables (e.g. pregnancy rate and litter size) are not well documented. Moreover, in these studies differences in energy balance are induced by restricted feeding of sows, which might be different from 'natural' differences in energy balance.

Most of the studies above have focused on first litter (first parity) sows. First parity sows are especially sensitive to body reserve depletion because they do not have enough body reserves at first farrowing and their feed intake capacity is not sufficient to fulfill energy needs during lactation (Everts, 1994). In addition, young sows still need to grow to reach maturity. Growth mainly consists of protein and fat accretion and aims to reach a certain 'intrinsic growth standard' (Everts and Dekker, 1995). The lack of body reserves and desire to grow, make young sows more sensitive to the negative effects of a negative energy balance on reproduction (Prunier et al., 2003).

This retrospective study aims to quantify the association between reproductive performance of second parity sows, focusing on non-pregnancy and litter size in relation to measures of sow live weight development in first parity.

2. MATERIALS AND METHODS

2.1 General

Between August 1999 and June 2005, sow development and sow reproduction data were recorded on a routine basis on two experimental farms of Wageningen University and Research Centre in The Netherlands. Farm A had a sow population of about 400 Great Yorkshire×Dutch Landrace sows (Y×DL). Farm B had a sow population of about 300 sows, consisting of Dutch Landrace (DL) and Y×DL sow lines.

During lactation sows were housed in individual farrowing crates and were fed a commercial lactation diet. After a gradual increase in feeding level during the first week of lactation, sows were fed ad libitum for the remaining lactation. Actual feed intake per sow was not recorded. During the weaning to insemination interval, sows were individually housed in crates and were fed a commercial gestation diet with a maximum of 3.5 kg of per day. Sows were checked for estrus twice a day using a mature boar. On the first day of standing estrus sows were inseminated using a commercial AI dose. A second insemination took place when the standing estrus extended to the next day. An ultrasound pregnancy check was done 4 weeks after insemination. During pregnancy sows were housed in stable groups with either feeding stalls (farms A and B) or feeding stations (farm A). Sows were fed a commercial gestation diet. Feeding level on farm A was 2.5 kg per day for the first 60 days of gestation, 2.8 kg per day from days 61 to 85, and 3.4 kg per day from day 86 for the remaining gestation. Feeding level for farm B was 2.6 (parity 1) or 2.8 (parity >1) kg per day for the first 85 days of gestation, and 3.0 (parity 1) or 3.4 (parity 2) kg per day for the remaining gestation.

2.2 Measures of sow development

Measures of sow development, both body weight and back fat, were taken throughout sow reproductive life. Both farms recorded age and body weight at first insemination, body weight at day 112 of pregnancy and body weight at weaning. On farm A also back fat was measured (P2method) at first insemination, at day 112 of pregnancy and at weaning. Based on body weight and back fat, the protein content of sows on farm A was estimated according to the formula of Everts and Dekker (1995):

Protein (kg)=1.67+0.175 × weight (kg) – 0.38 × P2 (mm).

Weight after farrowing (kg) was estimated as: Weight after farrowing (kg) =
weight at day 112 of prenancy (kg) – (total number of piglets born × 1.5 kg).

The 1.5 kg accounts for the estimated average piglet weight at birth including placenta and fluids.

2.3 Sow reproduction measurements

For each sow, weaning to insemination interval (WII), number of piglets born alive, number of piglets born dead, and number of piglets weaned were recorded per parity. Total number of piglets born (TNB) was calculated from number born alive and number born dead. Only on farm A individual sow records of cross-fostering and piglet birth weight were registered. A sow was considered pregnant after a positive pregnancy diagnosis at 4 weeks from after insemination.

2.4 Statistical analyses

Differences between parities and between farms in sow development and reproduction variables were tested for significance using general linear regression (proc glm, SAS Inst. Inc., 2004). Assumptions on normality were checked by examining model residuals.

Effects of sow development on reproductive performance were analyzed using two outcome variables. A binary outcome variable 'non-pregnancy' (yes/no) was analyzed using logistic regression (proc logistic, SAS Inst. Inc., 2004). Total number born in second parity (TNB2) was analyzed using general linear regression (proc glm, SAS Inst. Inc., 2004), in which assumptions on normality were checked by examining model residuals. Repeat breeders were omitted from the analysis on TNB2, since a prolonged (recovery) period between weaning and conception can positively influence litter size and therefore mask possible effects on litter size (Revell et al., 1998; Prunier et al., 2003). Reason of culling was not registered properly on both farms and, therefore, no statistical inferences on culling could be made.

Explanatory variables tested were: age and weight at first insemination; weight at first farrowing; weight gain during first pregnancy, weight loss during lactation, weight at first weaning, total number of piglets born in first parity, number of piglets weaned in first parity, season of insemination and farrowing, sow line (only farm B) and housing during gestation (only farm A). If explanatory variables, measured on a continuous scale, were linearly related to the dependent variable they were analyzed as continuous variables. If independent variables were not linearly related to the dependent variable, they were categorized and analyzed as class variables (weaning to insemination interval ($\leq$4, 5, 6–20, $\geq$21 days)), relative weight loss during lactation ($\leq$15% and >15%).

Including highly correlated variables in a multivariable model results in co-linearity problems. As a consequence of that, it might be difficult to statistically select the most "important" predictors from a larger group of explanatory variables. This is less serious if the purpose of analysis is prediction, but it is a problem when interpretation of causal effects is the objective (Hosmer and Lemeshow, 1989). To avoid co-linearity problems in multivariable models, only variables with a Pearson correlation coefficient of <0.5 (Table 2.1) were included in the multivariable model.

If variables were highly correlated, the variable that correlated with the highest number of other variables was chosen to be included in the multivariable model. Minimizing the number of variables results in a model that is numerically stable, and reduces the standard errors (Neter et al., 1985). As our goal was not prediction, and due to high correlations between explanatory variables associated with non-pregnancy, also results of univariable analyses are presented. All variables possibly affecting TNB2, as well as two-way interactions, were included in a multivariable model. In a backward elimination procedure, the least significant interaction or variable was eliminated from the model until the final model only contained significant (P≤0.05) variables.

Non-pregnancy results are presented as percentage of non-pregnancy, odds ratio (OR) and 95% confidence interval (CI). An OR is an estimate of the relative risk, which is the prevalence or cumulative incidence in the 'exposed' group divided by the prevalence of cumulative incidence in the reference group. If an OR equals 1, then there is no association between the variable and the outcome variable; if OR is smaller than 1, the variable imposes a decreased risk; if OR is larger than 1 the variable imposes an increased risk (Frankena and Thrusfield, 2001). In the results section of this paper, only variables significantly (P<0.05) associated with non-pregnancy and TNB2 are presented.

3. RESULTS

3.1 Measures of sow development

Farms differed significantly in sow live weight development (P < 0.05, Table 2.2) and were therefore analyzed separately. Age and weight at first insemination were 46 days and 21.3 kg lower at farm A compared with farm B. After first farrowing and at first weaning sows on farm A remained lighter, but the weight difference was reduced from 21.3 kg at first insemination to 9.5 kg at first weaning. Both absolute and relative weight loss during lactation, was similar for farm A (24.9 kg and 13.6%) and farm B (23.7 kg and 12.3%). On average, sows on farm A gained more weight in the period between first insemination and first weaning compared with farm B (31.6 kg for farm A, 20.9 kg for farm B; P < 0.05).

3.2 Reproduction measurements

Table 2.3 shows reproduction results for the first two parities per farm. Pregnancy rates of first and second parity did not differ between farms. On farm A pregnancy rate was similar for both parities (resp. 88.5 vs. 88.7% for parities 1 and 2).On farm B, however, pregnancy rate of second parity was 4.2% lower (P < 0.05) compared with first parity (84.2% vs. 88.4%). Total number born in first parity sows was 1.1 piglet lower (P < 0.05) for farm A compared with farm B (10.7 vs.11.8), whilst total number born in second parity did not differ between farms (both 11.6). On farm A total number born was 0.9 piglet higher (P < 0.05) in second parity compared with first parity sows (11.6 vs. 10.7).

Table 2.1 Pearsons correlation coefficients between sow development[1] and reproductive performance in first and second parity sows

Farm A	TNB1	TNB2	Weaned1	age1stbr	wfirstbr1	wdiffpreg	wafterfar1	wwean1	wloss	wdiff1
TNB1	1									
TNB2	0.05	1								
weaned	0.57*	-0.04	1							
age1stbr	0.05	-0.01	0.04	1						
wfirstbr1	0.09	-0.11	0.03	-0.06	1					
wdiffpreg	0.16*	0.05	0.09	0.30*	-0.11*	1				
wafterfar1	-0.06	-0.06	-0.04	0.24*	0.43*	0.80*	1			
wwean1	-0.13*	0.08	-0.27*	0.18*	0.41*	0.43*	0.67*	1		
wloss	0.07	-0.14*	0.30*	0.04	-0.04	0.40*	0.33*	-0.47*	1	
wdiff1	-0.19*	0.15*	-0.31*	0.23*	-0.13*	0.55*	0.49*	0.85*	-0.50*	1

Farm B	TNB1	TNB2	weaned	age1stbr	wfirstbr1	wdiffpreg	wafterfar1	wwean1	wloss	wdiff1
TNB1	1									
TNB2	0.22*	1								
weaned	0.11*	-0.06	1							
age1stbr	0.15*	0.13*	0.03	1						
wfirstbr1	0.09	0.06	0.02	0.32*	1					
wdiffpreg	0.19*	0.06	0.06	-0.20*	-0.28*	1				
wafterfar1	-0.02	0.04	0.04	0.15*	0.52*	0.64*	1			
wwean1	0.02	0.14	-0.24*	0.06	0.30*	0.42*	0.60*	1		
wloss	-0.05	-0.08	0.18*	0.10	0.26*	0.20*	0.41*	-0.47*	1	
wdiff1	0.00	0.09	-0.27*	-0.25*	-0.41*	0.60*	0.19*	0.74*	-0.63*	1

[1] TNB1 = total number of piglets born in first parity, TNB2 = total number of piglets born in second parity, age1stbr = age at first insemination
wbirstbr1 = weight at first insemination, wdiffpreg= weight difference from first insemination to first farrowing, wafterfar1 = weight after first farrowing
wwean1= weight after first weaning, wloss = weight loss during first lactation, wdiff1 = weight difference from first insemination to first weaning

* indicates significant correlations

On farm B total number born did not significantly differ between second and first parity (11.6 and 11.8). Number of piglets weaned in first and second parity did not differ between or within farms. Weaning to insemination interval was 2 days longer (P < 0.05) on farm A compared with farm B, respectively 8 and 10 days.

3.3 Factors associated with non-pregnancy

For farm A, measures of sow live weight development were associated with non-pregnancy (Table 2.4), whilst other variables were associated with non-pregnancy on farm B (Table 2.5). For both farms, weight gain from first insemination to first weaning was associated with a decreased percentage of non-pregnancy, i.e. an increased pregnancy rate. Each 10 kg increase in weight gain between first insemination and first weaning decreased the percentage of non-pregnancy on both farms (OR = 0.72 for farm A (P = 0.02) and OR= 0.76 for farm B (P = 0.001)). To visualize this, Fig. 2.1 shows how to interpret an OR of a continuous explanatory variable, in this case the OR per 10 kg weight gain from first insemination to first weaning. It shows how much the percentage of non-pregnancy decreases per unit of weight gain. For example farm A, the difference in percentage of non-pregnancy for sows that gain 20 kg compared to sows that gain 30 kg is 3.4% (15.7% vs. 12.3% non-pregnancy, respectively). If the weight gain increases from 20 to 50 kg, the percentage of non-pregnancy decreases from 15.7 to 7.4%.

For farm A, higher weight at first weaning was associated with a decreased percentage of non-pregnancy (OR = 0.76 per 10 kg; P = 0.03), whilst weight loss during first lactation was associated with an increased percentage of non-pregnancy (OR = 1.79 per 10 kg; P = 0.001). Relative weight loss was also associated with non-pregnancy, sows losing more than 15% of their weight during lactation had an increased percentage of non-pregnancy compared to sows losing less than 15% of their weight (OR = 2.82, P = 0.02). After a multivariable analysis only weight gain from first insemination to first weaning remained in the model. For farm B, sow line was associated with 24.5% non-pregnancy in Dutch Landrace compared with 14.2% in the crossbreed (Y×DL) (OR = 1.96; P = 0.001). Higher weight at first insemination was associated with higher percentage of non-pregnancy (OR = 1.39 per 10 kg; P = 0.015). A weaning to insemination interval of 6–20 days was associated with an increased percentage of non-pregnancy (29.2%) compared with a WII of 5 days (10.9%; OR= 3.39; P = 0.001). Season also affected farrowing rate, since both farrowing and being bred in summer compared with winter were associated with an increased percentage of non-pregnancy (respectively 25.0%, OR= 2.76; P = 0.001 and 23.8%, OR= 2.97; P = 0.001). After a multivariable analysis only weight gain from first insemination to first weaning remained in the model.

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Table 2.2 Measures of sow development from first insemination to first weaning on two farms

Variable	Farm A			Farm B		
	Mean	SEM	N	Mean	SEM	N
Age at 1st insemination (dys)	229.4[a]	0.6	340	275.4[b]	0.9	767
Weight at 1st insemination (kg)	123.9[a]	0.5	340	145.2[b]	0.8	284
Weight gain during 1st pregnancy (kg)	73.2[a]	0.8	301	62.1[b]	1.0	218
Protein gain during 1st pregnancy (kg)	10.6	0.1	277	nd	nd	-
Weight after farrowing (kg)	180.9[a]	0.9	301	189.4[b]	1.1	257
Weight at weaning (kg)	156.0[a]	0.9	301	165.5[b]	1.1	236
Weight loss 1st lactation (kg)	24.9	0.7	301	23.7	1.0	236
Protein loss 1st lactation (kg)	2.2	0.1	263	nd	nd	-
Backfat loss 1st lactation (mm)	5.9	0.1	283	nd	nd	-
Relative weight loss 1st lactation (%)	13.6	0.4	301	12.3	0.5	236
Relative protein loss 1st lactation (%)	8.1	0.5	263	nd	nd	-
Weight gain from 1st insemination to 1st weaning (kg)	31.6[a]	0.8	340	20.9[b]	1.3	216

[a,b] different superscripts within rows indicate significant differences (P<0.05), nd = not determined

Table 2.3 Reproduction results of first and second parity sows

Parity	1			2		
Variable	Mean	SE	N	Mean	SE	N
Farm A						
Pregnancy rate (%)*	88.5		340	88.7		301
Total born (n)**	10.7[ax]	0.1	301	11.6[b]	0.2	267
Born alive (n)**	10.3[ax]	0.1	301	11.2[b]	0.2	267
Weaned/sow (n)	10.0	0.1	300	10.4	0.1	267
Lactation length (dys)	29.2[a]	0.2	340			
WII (dys)	-	-	-	10.0[x]	0.6	271
Farm B						
Pregnancy rate (%)*	88.4		767	84.2		638
Total born (n)**	11.8[y]	0.1	640	11.6	0.1	513
Born alive (n)**	11.1[y]	0.1	640	11.2	0.1	513
Weaned/sow (n)	9.8	0.1	640	10.5	0.1	513
Lactation length (dys)	25.7	0.2	711			
WII (dys)	-		-	8.0[y]	0.3	638

[a,b] different superscripts within rows indicate significantly differences (P<0.05); [x,y] different superscripts within columns indicate significantly differences between farms (P<0.05); * only significant between parity 1 and 2 on farm B; ** from 1st insemination

Table 2.4 Univariable odds ratios for variables associated with non-pregnancy in second parity sows of Farm A

Variable	Category	N	Non-pregnancy (%)	Odds Ratio	95% CI	P-value(-2 log likelihood)
Weight at first weaning (per 10 kg)	Cont.[1]	271	10.7	0.76	0.58 - 0.98	0.03
Weight gain 1st insemination to 1st weaning (per 10kg)[†]	Cont.[1]	271	10.7	0.72	0.55 - 0.96	0.02
Weight loss during 1st lactation (per 10kg)	Cont.[1]	237	10.7	1.79	1.26 - 2.55	0.001
Relative weight loss 1st lactation (%)	≤15.0	147	6.1	Ref		0.02
	>15.0	90	15.5	2.82	1.17 - 6.83	

[1] cont. = continuous, for mean per variable see Table 2.2, [†] variable that remained significant after multivariable regression

Table 2.5 Univariable odds ratios for variables associated with non-pregnancy in second parity sows of Farm B

Variable	Category	N	Non Pregancy (%)	Odds Ratio	95% CI	P-value (-2 log likelyhood)
Sow Line	DL	102	24.5	1.96**	1.17 - 3.28	0.001
	Y*DL	536	14.2	Ref		
Weight at first insemination (per 10 kg)	Cont.[1]	233	15.5	1.39	1.06 - 1.81	0.015
Weight gain from 1st insemination to 1st weaning (per 10 kg)†	Cont.[1]	203	16.2	0.76	0.61 - 0.95	0.001
Weaning to insemination interval (days)	≤4	110	16.4	1.61	0.85 - 3.03	
	5	267	10.9	Ref		0.0047
	6-20	194	22.7	2.41**	1.44 - 4.02	
	≥21	67	14.9	1.44	0.66 - 3.12	
Season of 1st farrowing	Fall	118	14.4	1.39	0.71 - 2.74	
	Spring	176	15.3	1.50	0.82 - 2.74	
	Summer	140	25.0	2.76**	1.54 - 4.94	
	Winter	204	10.8	Ref		0.006
Season of 2nd insemination	Fall	119	20.2	2.41*	1.23 - 4.71	
	Spring	176	11.9	1.29	0.66 - 2.54	
	Summer	164	23.8	2.97**	1.61 - 5.50	
	Winter	179	9.5	Ref		0.001

* $P < 0.05$, ** $P < 0.001$: levels of significance of the Wald's P-value for the category compared to the reference (Ref) category

[1] cont. = continuous, for mean per variable see Table 2.2, † variable that remained significant after multivariable regression

Farm A (n=271) ——— Farm B (n=203) - - - - -

probability of being non-pregnant:

Farm A: $1/(1 + \exp^{(1.124 + 0.028*weight\ gain)})$

Farm B: $1/(1 + \exp^{(1.184 + 0.033*weight\ gain)})$

Non-pregnancy (%)

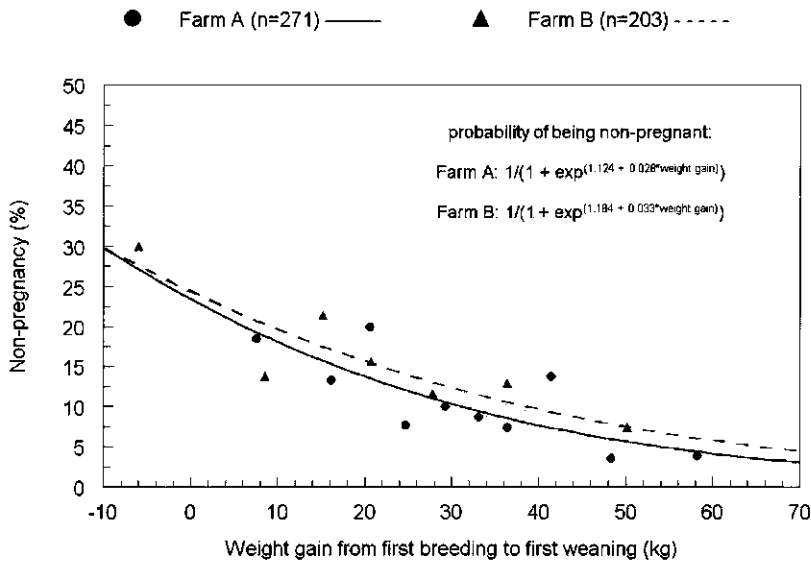Weight gain from first breeding to first weaning (kg)

Figure 2.1 Relation between weight gain from first insemination to first weaning and probability of non-pregnancy (lines are estimated by logistic regression each marker represents observed values of about 30 sows)

3.4. Factors associated with total number born in second parity (TNB2)

For farm A, 11 explanatory variables were eligible for multivariable analysis, however due to high correlations 5 variables were not included; number of piglets weaned in first parity was correlated with total number of piglets born in first parity (r = 0.57, Table 2.1), weight gain from first insemination to first weaning was correlated with weight difference during pregnancy, weight after farrowing, weight loss during lactation and weight at weaning (resp., r = 0.55, 0.49, –0.50 and 0.85, Table 2.1).

The multivariable model, therefore, started with 6 variables; total number of piglets born in first parity (TNB1), weight gain from first insemination to first weaning, weight at first insemination, age at first insemination, season of insemination in second parity and weaning to insemination interval in second parity (WII2). The final model contained 3 variables with no significant interaction effects; TNB1, weight gain from first insemination to first weaning and WII2 (Table 2.6, R2 = 0.08). For every piglet born in first parity TNB2 increased with 0.18 piglet (P = 0.04). Per 10 kg higher weight gain from first insemination to first weaning TNB2 increases with 0.42 piglet (P = 0.008).

Table 2.6 Effects on total number of piglets born in second parity: multivariable model estimates for continuous variables and Least Square Means (LSmeans) for class variables

Variable	Class	Farm A		Farm B	
		Estimate (SE)	P-value	Estimate (SE)	P-value
Intercept		9.32 (0.61)	<0.001	11.03 (0.61)	<0.001
Total number born in 1st parity (n)	Cont.	0.18 (0.09)	0.04	0.27 (0.10)	<0.001
Weight gain from 1st insemination to 1st weaning (per 10 kg)	Cont.	0.42 (0.16)	0.008		ns
		Estimate (SE)	P-value	Estimate (SE)	P-value
Weaning to insemination interval (days)	≤4	11.0 (0.5)[ab]	0.01	11.8 (0.6)[yz]	0.03
	5	12.2 (0.3)[ab]		11.5 (0.4)[z]	
	6-20	10.9 (0.4)[b]		11.1 (0.5)[z]	
	≥21	12.5 (0.4)[a]		14.2 (0.9)[y]	

ns = not significant; [a,b] different subscripts within columns tend to indicate significant differences (P < 0.10)

[y,z] different subscripts within columns indicate significant differences (P < 0.05)

R^2 of the model is 0.08 for Farm A and 0.11 for Farm B

Sows with a WII2 of more than 21 days tended (P = 0.08) to have higher TNB2 compared with sows with a WII2 of 6–20 days (resp. 12.5 vs. 10.9 piglet). For farm B also 11 explanatory variables were eligible for multivariable analysis, however due to high correlations 4 variables were not included; weight at first breeding was correlated with weight after first farrowing (r = 0.52, Table 2.1), weight gain from first insemination to first weaning were correlated with weight loss during lactation and weight at weaning (resp., r =−0.63, r = 0.74, Table 2.1). The multivariable model therefore started with 7 variables; TNB1, weight gain from first insemination to first weaning, age at first insemination, weight after

first farrowing, number of piglets weaned in first parity, season of insemination in 2nd parity and WII2. The final model contained 2 variables; TNB1 and WII2 (Table 2.6, R2 = 0.11). For every extra piglet born in first parity TNB increased with 0.27 piglets in second parity. Sows with a WII2 of more than 21 days had more piglets in second parity compared to sows with a WII2 of 5 or 6–20 days (resp. 14.2, 11.5 and 11.1 TNB2). Interaction was not significant.

4. DISCUSSION

The aim of this study was to quantify the association between reproductive performance of second parity sows, focusing on non-pregnancy and litter size in relation to measures of sow live weight development in first parity. Reproductive performance of second parity sows is related with several variables such as lactation weight loss (Morrow et al., 1989; Thaker and Bilkei, 2005) and weaning to insemination interval in second parity (WII2,Vesseur, 1997). A high lactation weight loss has been reported to decrease litter size and pregnancy rate in subsequent parity (Thaker and Bilkei, 2005) and to increase WII2 (Vesseur, 1997). In our study many variables concerning live weight development were associated with non-pregnancy and litter size in second parity. However, many of these variables are highly correlated and cannot be analyzed in a multivariable model. This is not a problem when prediction is the goal of the study (Hosmer and Lemeshow, 1989). As our goal is not to predict, but to explain differences caused by causal factors, we will also discuss the results of single predictors. From these data it cannot be judged which explanatory variable is most important in explaining differences.

In our study, weight gain from first insemination to first weaning affected pregnancy rate in second parity on both farms and litter size in second parity on farm A and therefore seems to be an important variable affecting reproductive performance in second parity. One should note, however, that for the analysis on TNB2 the R2 for the final models was rather low, indicating that there should be also other factors, though not measured in the study, affecting litter size in second parity. Weight gain from first insemination to first weaning represents the growth of an animal during the first cycle and is a combined effect of weight gain during pregnancy (r = 0.55) and weight loss during lactation (r = 0.50). Replacing weight gain from first insemination to first weaning with the two variables weight gain during pregnancy and weight loss during lactation resulted in non-significant effects for both variables (results not shown). Weight gain from first insemination to first weaning, therefore, appears to be a better explanation for TNB2 than each variable separately.

Positive effects of weight gain between first insemination and first weaning on reproduction results might be explained by the desire of young animals to grow to a certain mature size. Selection on lean growth has led to a gilt which is physiologically immature at time of first insemination (Everts, 1994). Therefore, gilts and young sows still need to grow to reach their mature weight and body composition, perhaps by aiming to reach a certain intrinsic target (Clowes et al., 1994; Everts and Dekker, 1995). If this growth is not achieved between

first insemination and first weaning a gilt might prioritize growth above reproduction after weaning, which can result in non-pregnancy or reduced litter sizes in second parity compared with first parity. Our data show that the percentage pregnancy increases when weight gain between first insemination and first weaning increases. This substantiates the hypothesis that intrinsic growth of a, relative, immature gilt to mature size, can be a factor involved in poor reproductive performance in second parity sows.

Weaning to insemination interval also affected reproductive performance of second parity sows on both farms; sows with an interval ≥21 days showed higher litter sizes in second parity compared with sows with an interval of 6–20 days. Similar results have been reported by Vesseur (1997) and Morrow et al. (1989). By extending the period between weaning and insemination sows have time to recover from lactation weight loss and will therefore show better reproductive performance (Morrow et al., 1989).

The lower production of first parity sows on farm A compared to farm B might be related to the difference in age (and possibly weight) at first insemination between both farms. Le Cozler et al. (1998) and Schukken et al. (1994) both showed that sows older than 270 days at first mating or conception produced more piglets born alive in first parity. The relation between litter size in first parity and litter size in second parity on both farms might be explained by a high genetic correlation between litter size in first and litter size in second parity (Hanenberg et al., 2001). Phenotypic correlation, however, was low (r = 0.05 for farm A and 0.22 for farm B) as is also described by Hanenberg et al. (2001). The strong effect of sow development on reproduction performance of second parity sows on farm A could also be related to the fact that gilts on farm B were heavier and older at first insemination compared with gilts on farm A. First parity sows are especially sensitive to body reserve depletion during first lactation. They do not have enough body reserves at first farrowing and their feed intake capacity is not sufficient to fulfil energy needs during lactation (Mejia-Guadarrama et al., 2002). A heavier and older gilt at first insemination is probably also heavier at first farrowing (r = 0.43 for farm A and r = 0.53 for farm B, Table 2.1), and therefore better able to cope with the negative energy balance during lactation (Gill, 2000). The results show that relations between live weight development and reproduction in first parity and subsequent reproduction in second parity differ between the two farms. It indicates that management factors like age and weight at first insemination and probably many other factors affect these relations. Farm management strategies should therefore always be taken into account when trying to assess generalized associations between live weight development, reproduction in first parity and subsequent second parity reproduction results.
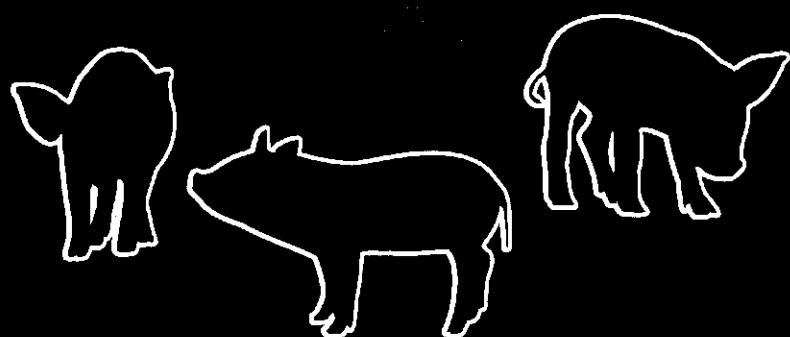
Exclusion of repeat breeders for analysis on litter size is important to determine the true difference of litter sizes between parities, since repeat breeders often have larger litter sizes compared with non-repeat breeders (Tummaruk et al., 2001b). For example, litter sizes for second parity sows including repeat breeders would have been 0.2 piglet higher for farm A (11.8 vs. 11.6) and 0.3 piglet higher for farm B (11.9 vs. 11.6) compared with litter sizes of second parity sows not including repeat breeders. Sow management programs, however,

do not separately show litter sizes from first insemination, and therefore the true effects of first cycle on reproductive performance in second parity is masked. Adding litter size after first insemination to sow management programs might thus provide valuable information for farmers and their advisors.

The results described in this study, show that gilts that are relatively light or young at first insemination have reduced reproductive performance in first parity. For these sows, sow live weight development has a large influence on reproductive performance in second parity. Management of these animals should aim to optimize development at first insemination and to increase growth between first insemination and first weaning, for example by increasing growth during pregnancy or reducing weight loss during first lactation, in order to optimize production in second parity.
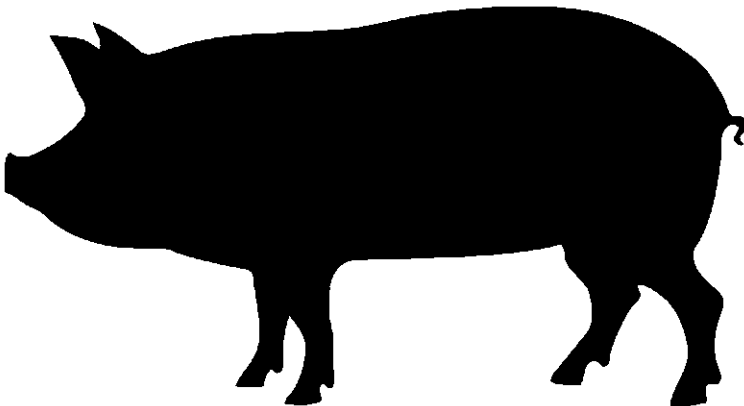
Acknowledgements

Chapter 3

Lactation weight loss in primiparous sows: consequences for embryonic survival and progesterone and relations with metabolic profiles

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Lactation weight loss in primiparous sows: consequences for embryo survival and progesterone and relations with metabolic profiles

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ABSTRACT

Our objective was to study reproductive consequences of lactation body weight loss occurring in primiparous sows with mild feed restriction and to relate these lactation weight losses and its consequences to metabolic profiles during lactation and subsequent early gestation. After weaning, 47 first litter sows were retrospectively assigned to a high (HWL, > 13.8%, n=24) or low (LWL, ≤ 13.8%, n=23) weight loss group. Thirty-six animals received an indwelling jugular vein catheter to determine lactational and gestational profiles of Insulin-like Growth Factor-1 (IGF-1), Non-Esterified Fatty Acids (NEFA) and urea and gestational profiles of progesterone. At day 35 after insemination sows were euthanized and their reproductive tract collected. Pregnancy rate was 75% (18/24) for HWL and 96% (22/23) for LWL sows. High weight loss sows had a lower number of implantation sites (17.2 ± 0.8 vs. 19.5 ± 0.7, respectively, p = 0.03) and a lower embryonic survival (65.6 ± 3.4 vs. 77.4 ± 2.9%, P = 0.02), resulting in fewer vital embryos (14.9 ± 0.9 vs. 16.8 ± 0.7, P = 0.07) than LWL sows. Progesterone peak values were reached later in HWL than in LWL sows (day 13.4 ± 0.5 vs. 12.0 ± 0.5, respectively, P = 0.05). Gestational concentrations of IGF-1, NEFA and urea were almost identical for HWL and LWL sows, whilst numerical differences were seen during lactation. The current study shows negative consequences of lactational weight loss in mildly feed restricted primiparous sows for embryonic survival, and showed that these consequences seem only mildly related with metabolic alterations during lactation and not with metabolic alterations during subsequent gestation.

Keywords: Lactation, Weight Loss, Reproduction, Metabolic Profiles, Primiparous Sows

1. INTRODUCTION

During lactation, feed intake of sows is often not sufficient to fulfil the energy demands for maintenance and milk production (Eissen et al., 2003). To ensure sufficient milk production, sows utilize their body reserves, i.e. protein and fat, as an energy source for milk (Noblet et al., 1998). These lactational body weight losses negatively influence farrowing rate and litter size in subsequent parity (Prunier et al., 2003; Schenkel et al., 2010). Especially primiparous sows have substantial lactational losses since their feed intake capacity is often lower compared with multiparous sows (Quesnel, 2009). Furthermore, primiparous sows have relatively limited body reserves and still need to grow to reach mature size and therefore might be more sensitive to the negative effects of lactation losses on reproduction.

Several authors have studied the physiological mechanisms through which lactation weight loss in primiparous sows can affect reproductive performance, using restricted feeding. From these studies negative effects on ovulation rate (Zak et al., 1997a; van den Brand et al., 2000c), oocyte quality (Zak et al., 1997b) and embryonic survival (Baidoo et al., 1992b; Vinsky et al., 2006) are reported. These negative effects of feed restriction on follicular development and oocyte quality are mediated by several hormonal and metabolic changes during lactation in response to the catabolic state of the sow as reviewed by Quesnel (2009). Feed restricted lactating sows, or sows in a negative energy balance, show low plasma glucose, insulin and Insulin like Growth Factor-1 (IGF-1) concentrations (Zak et al., 1997a) and high Non Esterified Fatty Acids (NEFA) concentrations (Hultén et al., 2002a). Insulin and IGF-1 can act on the hypothalamus and thereby affect LH release (Quesnel and Prunier, 1998; Van Den Brand et al., 2001b). Low insulin and IGF-1 concentrations, however, can also reduce follicular development through direct effects on the ovaries (Quesnel, 2009). Further, in dairy cattle, high NEFA concentrations have shown to be detrimental to embryonic survival by influencing oocyte quality, the embryonic environment or both (Leroy, 2005).

The above described relationships have been established in experiments that used severe feed restriction during lactation and have focussed only on metabolic consequences during lactation. Therefore, the aim of the current paper is to study the reproductive consequences of lactational bodyweight loss in sows with mild feed restriction and to relate both weight loss and its consequences to metabolic profiles during lactation and subsequent early gestation.

2. MATERIALS AND METHODS

All experimental procedures were approved by the Institutional Animal Use and Care Committee of Wageningen University (Wageningen, The Netherlands).

2.1 Animals, housing, feeding and treatment

In total 47 crossbred (Yorkshire x Dutch landrace) first parity sows were used. Between October and December 2010, the animals arrived in three consecutive batches (n = 14, n = 17 and n =16, respectively) at day 80 ± 4 of first gestation at the experimental farm 'de Haar' of Wageningen University in Wageningen, The Netherlands.

On day 103 ± 0.5 of first gestation, 36 sows were fitted with an indwelling jugular vein catheter as described by Soede et al. (1997), to allow frequent blood sampling. After surgery, all sows were housed in individual farrowing crates.

After placement in farrowing crates, gestation feed (12.2 MJ ME / kg, 13.0% crude protein and 0.3% lysine) was gradually replaced with the commercial lactation diet (13.1 MJ ME / kg, 15.5% crude protein and 0.8% lysine) which was fed throughout lactation. Throughout the experiment, animals were fed twice a day (0830 and 1600 h) and had ad libitum access to water. Within 3 days after farrowing, litters were standardized to 11 - 14 piglets. Daily feed allowance gradually increased in the first 14 days of lactation to a maximum of 7 kg, which was based on sow body weight after farrowing and number of piglets suckling (1% of body weight for maintenance and 0.4 kg per piglet). During lactation, wet weight of feed refusals was determined and classified as low (<1 kg) or high (≥1 kg). After weaning (25.5 ± 1.4 days after farrowing), sows were housed in individual gestation crates. From weaning to insemination, sows were fed 3.5 kg/day of the lactation diet. Sows were checked for estrus 2 times per day (0900 h and 1530 h) using the back pressure test in the presence of a mature teaser boar. Four to 6 h after first standing estrus, sows were inseminated with a commercial dose of semen (1.5 x 109 motile sperm cells of a TOPIGS boar line, Topigs, Vught, The Netherlands). If still in estrus, sows received a second or third insemination 21 to 24 hours after first or second insemination.

From day 3 after first insemination sows received either 2.5 or 3.25 kg of a standard gestation feed (12.2 MJ ME, 13% crude protein, 0.29% lysine) per day. From day 18 after first insemination onwards, sows were checked for signs of estrus twice a day using fence line contact with a mature teaser boar. Date of return to estrus was recorded as the date the first standing reflex was observed. Around 4 weeks of gestation an ultrasound check (Scanner 200, Pie Medical/Esaote, Maastricht, The Netherlands) was performed to confirm pregnancy.

Retrospectively, based on the median of the percentage of weight loss during lactation, sows were divided in a Low Weight Loss (LWL, ≤ 13.8%, n=23) or High Weight Loss (HWL, > 13.8%, n=24) group. Only pregnant sows (n=22 for LWL, n= 18 for HWL) were used to study effects of lactation weight loss on metabolic, hormonal and reproductive parameters.

2.2 Measurements

Sow body weight, backfat and loin muscle depth were measured one day after farrowing and at weaning. Back fat was measured 6 cm of the midline, straight above the last rib

on the left and right sides of the animal using a Renco© Meter (MS Schippers, Bladel, The Netherlands). In animals from batch 2 and 3, loin muscle depth was measured at the same locations using Aloka Ultrasound Equipment (Aloka SSD-500, Biomedic Nederland BV., Almere, The Netherlands). For loin muscle measurement, two measurements were taken on both the left and right sides of the animal. If the two measurements at one side differed more than 2 mm, a third measurement was taken. Piglets were weighed on day 3 after farrowing, week 3 of lactation and at weaning and litter weight was calculated by adding the weights of all piglets in a litter at the different times the piglet were weighed.

2.2.1 Blood sampling

On days 10, 6 and 3 before weaning and the day of weaning, 10 ml blood samples were taken at 0730 h, for analysis on IGF-1, NEFA, urea and leptin.

From day 4 until day 25 after weaning, 3 ml blood samples were taken daily at 0730 h. After day 25, blood samples were taken three times per week, at 2 to 3 day intervals up until slaughter. These samples were analyzed for progesterone. From day 4 till day 25 after weaning an additional 7 ml blood sample was taken twice a week (at 3 to 4 day intervals) at 0730 h, for analysis of IGF-1, NEFA and urea.

All blood samples (except for NEFA samples) were collected in polypropylene tubes containing 50 or 100 µl (depending on sample size) EDTA solution (144 mg/ml saline), were placed on ice and centrifuged at 3000 x g for 10 min at 4°C. Plasma was collected and stored at -20°C until analysis. NEFA samples were collected in 0.8 ml serum tubes (Minicollect, Greiner Bio-One BV, Alphen a/d Rijn, Netherlands). After collection, the NEFA samples were allowed to incubate at room temperature for at least 1 h, after which the samples were centrifuged at 3000 x g for 10 min. Serum was collected and stored at -20°C until analysis.

2.2.2 Plasma analyses

Concentrations of plasma progesterone were analyzed in duplicate using a commercial Coat-A-Count Progesterone RIA-kit (PITKPG-7®, Siemens Medical Solutions Diagnostics, Los Angeles, CA, USA). The sensitivity, intra- and interassay CV were 0.1 ng/ml, 4.7 and 6.0% respectively. The average progesterone concentration was calculated as the mean of all values from days -1 to 34 (D1 = day of first progesterone rise above 0.5 mg/ml). Furthermore average progesterone concentrations from days 1 - 10, 11 - 15, 16 - 21 and 21 - 34 were calculated using all values in the defined time frame.

Concentrations of plasma IGF-1 were quantified in duplicate, using a commercial kit (IRMA IGF-1 A15729®, Immunotech, Marseille, France), after extraction of the samples with ethanol/HCl (as validated by Louveau and Bonneau (1996). The sensitivity, intra- and interassay CV were 2 ng/mL, 2.2% and 3.5%, respectively. NEFA concentrations were determined in duplicate using an enzymatic colorimetric assay using the Wako NEFA-HR (2) ACS-ACOD method (Wake chemicals, Neuss, Germany). One hundred microliters of Acetyl-CoA synthase was added to 5 µl serum and then incubated for 10 minutes at 37°C.

After incubation, 50 μl of Acetyl-CoA oxidase was added to the serum mixture and it was incubated again for 10 min at 37°C. After second incubation the extinction was measured with a spectrophotometer at a wavelength of 550 .nm, using a standard curve formula the NEFA concentration was calculated. The sensitivity of the test was 0.0014 mEq/l. Urea concentrations were also determined in duplicate using an enzymatic colorimetric assay (Urea liguicolor, Human, Wiesbaden, Germany), with a sensitivity of 0.1 mmol/l. Leptin was analyzed in duplicate using a commercial multi-species Leptin RIA-kit (Millipore, St .Charles, Missouri, USA). The sensitivity, intra- and interassay CV were 1.0 ng/ml, 3.2 and 7.8% respectively. Results of the leptin analysis are presented as ng/ml in human equivalent (HE). Average values for IGF-1, NEFA, urea and leptin during lactation were calculated by averaging the day -10, -6, -3 and 0 concentrations. Average values for IGF-1, NEFA and urea during gestation were calculated by averaging their respective concentrations on days 8, 11, 15, 18, 20, 25 and 40 concentrations.

2.2.3 Reproductive measurements
On the day after weaning, the diameter of the 5 largest follicles of the right ovary was determined by transcutaneous ultrasound scanning (Scanner 200; PieMedical / Esaote, Maastricht, The Netherlands). Weaning to estrus interval and date of return to estrus or confirmed non-pregnancy were recorded. At day 35.0 ± 0.6 of gestation, sows were slaughtered by stunning and exsanguination and their reproductive tracts were collected. The ovaries were removed and the number of corpora lutea counted. Luteal weight was determined after dissection of the corpora lutea from the ovaries. After removal of the mesometrium and separation of the uterine horns, the horns were cut open and the number of embryos were counted and classified as viable, based on size and color, or nonviable, based on strongly hemolyzed amniotic fluid, reabsorbed embryonic membranes or both. After separating embryos and placentas, length and weight of embryos and length of implantation sites was determined. Placental length was measured immediately and placental dry weight was determined after freeze drying for 72 h. Embryonic survival was calculated as the percentage of corpora lutea represented by a (vital) fetus (Jindal et al., 1997).

2.2.4 Statistical Analysis
Data were analyzed using SAS 9.2 (SAS Inst. Inc., Cary, NC, USA) and results are presented as LSmeans ± sem, unless stated otherwise. For all parameters, normality was checked using the UNIVARIATE procedure of SAS with a skewness and kurtosis between -2 and 2 considered to be normal. Pearson's correlation coefficients were used to determine relationships between continuous variables.
Lactation length, number of piglets weaned, litter growth and sow body weight, back fat and loin muscle depth development during lactation were analyzed using general linear regression (Proc GLM, SAS) with batch (1, 2, 3) and either pregnancy (yes or no) or, for pregnant sows only, weight loss class (LWL, HWL) as fixed effects.

Table 3.1 Weight, backfat and loin muscle development (LSMean ±SEM) for non-pregnant (NP) and pregnant (P) low weight loss (LWL, ≤13,77%) and pregnant high weight loss (HWL, >13,77%) sows

	Non-pregnant	Pregnant LWL*	Pregnant HWL*	P-value NP - P**	P-value LWL - HWL***
Number of Animals (n)	7	22	18	47	40
Weight loss (%)	19.0 ± 1.0[a]	11.0 ± 0.6[b]	17.6 ± 0.7[a]	0.006	<0.0001
Lactation length (days)	25.5 ± 0.5	25.7 ± 0.3	25.6 ± 0.3	0.77	0.76
Number of piglets weaned (n)	13.1 ± 0.4	12.5 ± 0.3	12.4 ± 0.3	0.14	0.81
Average piglet weaning weight (kg)	6.8 ± 0.25	6.4 ± 0.14	6.7 ± 0.15	0.42	0.10
Litter weight gain lactation (kg)	65.3 ± 2.6	60.9 ± 1.5	64.9 ± 1.6	0.38	0.09
Weight after farrowing (kg)	201.4 ± 4.3	198.7 ± 2.5	200.4 ± 2.7	0.69	0.71
Weight at weaning (kg)	163.5 ± 4.5[a]	176.7 ± 2.6[b]	165.0 ± 2.8[a]	0.16	0.001
Weight loss (kg)	37.8 ± 2.1[a]	21.9 ± 1.2[b]	35.3 ± 1.3[a]	0.007	<0.0001
Loin muscle depth at farrowing (mm)#	42.2 ± 1.6	40.0 ± 1.0	41.2 ± 1.1	0.38	0.29
Loin muscle depth at weaning (mm)#	31.0 ± 1.6	33.8 ± 0.9	31.1 ± 1.0	0.37	0.08
Loin muscle depth loss (mm)#	11.1 ± 1.5[a]	5.8 ± 0.9[b]	10.0 ± 1.0[a]	0.10	0.002
Back fat depth at farrowing (mm)	17.6 ± 0.9	17.7 ± 0.5	16.2 ± 0.6	0.58	0.07
Back fat depth at weaning (mm)	12.5 ± 0.9[ab]	13.1 ± 0.5[b]	11.4 ± 0.5[a]	0.85	0.03
Backfat depth loss lactation (mm)	5.1 ± 0.6	4.6 ± 0.3	4.8 ± 0.4	0.52	0.59
IGF-1 lactation (ng/ml)	nd	155.4 ± 10.7	133.6 ± 11.9	nd	0.20
NEFA lactation (µm/l)	nd	816 ± 67	989 ± 75	nd	0.10
Leptin lactation (ng/ml HE)	nd	3.1 ± 0.07	3.2 ± 0.08	nd	0.36
Urea lactation (mmol/l)	nd	4.8 ± 0.18	4.4 ± 0.20	nd	0.17

[a,b] variables for non-pregnant, LWL and HWL with different supersripts differ significantly, model with class (NP, LWL, HWL) and batch as fixed effects

* only pregnant sows, ** model with pregnant (yes/no) and batch as fixed effects,

*** model with lactation weight loss class (LWL and HWL) and batch as fixed effects, # n = 27

A third model analyzed differences between non-pregnant, pregnant LWL and pregnant HWL sows and also included batch as fixed effect. Interactions were tested in all models, but were never significant and therefore excluded from the model.

For pregnant animals, embryonic and placental characteristics and average IGF-1, NEFA urea and leptin concentrations during lactation and during gestation and average progesterone concentrations during gestation were analyzed using general linear regression (Proc GLM, SAS) with weight loss class (LWL, HWL) and batch (1, 2, 3) as fixed effects. Interactions were tested, but never significant and therefore omitted from the model. Since sows were fed different feeding levels during gestation, the effect of feeding level on reproductive performance and gestation metabolic hormone concentrations and the interaction of feeding level with lactation weight loss were tested. These were never significant and therefore only results from a model with weight loss and batch as fixed effects are presented. Sows were divided in two classes based on their feed refusals during lactation: 1) feed refusals never exceeded 1 kg wet weigh and 2) feed refusals exceeded 1 kg wet weight at least once. To test if the percentage of sows with feed refusals was different between HWL and LWL sows, a Chi-square test was used. In two of the pregnant animals the catheter did not function during part of the experiment; therefore they were excluded from analyses on metabolic parameters and progesterone.

Progesterone, IGF-1, NEFA and Urea profiles of pregnant animals were analyzed using Proc Mixed (SAS) with weight loss class (LWL, HWL) and day (-9, -5, -3, 0, 4, 8, 11, 15, 18, 20, 25, 40 for metabolites and d -1 to 21, 23, 26, 28, 30, 35 for progesterone) and their interaction as fixed effects. Sows was added as a repeated measure.

3. Results

3.1 Non-pregnant vs. Pregnant

In total 7 sows (6 HWL and 1 LWL) were not pregnant from insemination in the first estrus after weaning. Non-pregnant sows lost 4.8% more weight (18.8 ± 1.5 vs. 14.0 ± 0.7%, respectively, P = 0.006) and tended to lose more loin muscle (11.0 ± 1.7 vs. 7.8 ± 0.8 mm, respectively, P = 0.10) during lactation compared with pregnant sows, whilst back fat loss was not different between pregnant and non-pregnant sows (5.1 ± 0.6 vs. 4.7 ± 0.2 mm, respectively, P = 0.52). The interval from weaning to first insemination was also longer for non-pregnant than for pregnant sows (5.5 ± 0.3 vs. 4.7 ± 0.1 days, respectively, P = <0.0001), whilst lactation length (25.5 ± 0.5 vs. 25.7 ± 0.2 days, respectively, P = 0.78), number of piglets weaned (13.1 ± 0.4 vs. 12.4 ± 0.2 piglets, respectively, P = 0.14) and weight gain of the litter during lactation (65.3 ± 2.7 vs. 62.7 ± 1.1 kg, respectively, P = 0.38) were not different between non-pregnant and pregnant sows. Furthermore, non-pregnant sows had similar weight and loin muscle losses and similar weights at weaning as HWL sows, whilst

LWL sows had lower weight losses and loin muscle losses and a heavier weights at weaning compared with non-pregnant and HWL sows (Table 3.1).

3.2 High vs. Low weight loss

3.2.1 Sow body development and metabolic hormones during lactation
Table 3.1 shows lactation characteristics of non-pregnant sows and pregnant HWL and LWL sows. High weight loss sows had a 6.6% higher weight loss during lactation compared with LWL sows (p = <0.0001), resulting in a 11.9 kg lower weight at weaning (P = 0.001). Loin muscle loss was 4.2 mm higher for HWL sows than for LWL sows (P = 0.002), which resulted in a tendency for a 2.7 mm lower loin muscle depth at weaning (P = 0.08). Back fat depth at farrowing tended to be 1.5 mm less for HWL sows than for LWL sows. Back fat depth loss during lactation was similar for HWL and LWL sows, resulting in a 1.7 mm lower back fat at weaning for HWL compared with LWL sows (P = 0.03). Litter weight gain was higher for HWL than LWL sows during the first 3 weeks of lactation (45.6 ± 1.3 vs. 41.7 ± 0.9 kg, respectively, P = 0.03), but not in the last week of lactation (18.9 ± 0.6 vs. 18.9 ± 0.4 kg, respectively, P = 0.98), resulting in a tendency for a higher litter weight gain (+ 4 kg) for HWL compared with LWL sows (P = 0.09). The percentage of sows with one or more feed refusals exceeding 1 kg wet weight was higher in HWL than in LWL sows (78% (14/18) vs. 45% (10/22), respectively, P = 0.04).

3.2.2 Reproductive measures
Table 3.2 shows the reproductive measures on day 35 of gestation for HWL and LWL sows. Average follicle diameter on the day after weaning and the time from weaning to insemination were similar for pregnant HWL and LWL sows (Table 3.2). Ovulation rate was also similar for HWL and LWL, whilst number of implantation sites was 2.3 sites lower for HWL than LWL sows (P = 0.03). Vital embryonic survival was 11.8% lower for HWL than LWL sows (P = 0.01), resulting in a tendency for 1.9 fewer vital embryos at day 35 of gestation (P = 0.07). Furthermore, weight of vital embryos tended to be 0.5 g lower for HWL than for LWL sows (P = 0.07).

Concentrations of plasma progesterone increased to days 12 – 13 and then decreased to day 20 when they stabilized (Figure 3.1). Peak values of progesterone were similar for HWL and LWL sows (38.1 ± 2.5 vs. 37.4 ± 2.1 ng/mL, respectively, P = 0.83). However, progesterone concentrations in HWL sows took 1.4 day longer to reach their peak value than in LWL sows (13.4 ± 0.5 vs. 12.0 ± 0.4 days, respectively, P = 0.05). Average progesterone concentrations from day 0 to 10, 11 to 15, 16 to 21 and 22 to 35 were not different between groups (data not shown).

Table 3.2 Reproduction parameters for pregnant sows with a low (≤13.77%, average 11%) or high (>13.77%, average 17.6%) lactation weight loss

Variable	LWL	HWL	P-value
Number of animals (n)	22	17[#]	
Weaning to insemination interval (days)	4.8 ± 0.2	4.7 ± 0.2	0.81
Average follicle diameter at weaning (mm)	3.1 ± 0.07	3.1 ± 0.08	0.65
Ovary			
Number of CL (n)	21.9 ± 0.7	22.7 ± 0.8	0.47
Luteal Weight (g)	8.6 ± 0.3	8.2 ± 0.4	0.36
Number of embryo's			
Total (n)	18.9 ± 0.7[a]	16.1 ± 0.8[b]	0.02
Viable (n)	16.8 ± 0.7	14.9 ± 0.7	0.07
Numberof implantationsites (n)	19.5 ± 0.7[a]	17.2 ± 0.8[b]	0.03
Embryonic Survival			
Total (%)	86.7 ± 2.9[a]	71.1 ± 3.4[b]	0.002
Viable (%)	77.4 ± 3.0[a]	65.6 ± 3.4[b]	0.01
Viable embryos/implantation sites (%)	86.3 ± 2.2	88.4 ± 2.5	0.53
Embryonic Development			
Lenght (cm)	3.9 ± 0.07	3.7 ± 0.08	0.21
Weight (g)	4.5 ± 0.2	4.1 ± 0.2	0.09
Placental Development (Vital)			
Lenght (cm)	35.6 ± 1.4	38.3 ± 1.6	0.20
Dry weight (g)	2.0 ± 0.09	2.0 ± 0.09	0.56
Implantation Sites			
Lenght (cm)	20.5 ± 1.3	24.4 ± 1.4	0.06

[#] excluding one sow with 31 CL but only 3 embryos and 4 implantation sites

[a,b] different superscipt within a row differ significantly (P < 0.05)

3.2.3 Metabolic parameters

Plasma IGF-1 profiles were not different between LWL or HWL sows at any stage of lactation or gestation (Figure 3.2A). Average IGF-1 concentration during lactation was similar in HWL and LWL sows (Table 3.1) and was positively correlated with IGF-1 concentration during gestation (r = 0.46, P = 0.01).

Plasma NEFA profiles were similar for both groups of sows (Figure 3.2B). On d 5 before weaning NEFA concentration in HWL sows were higher than in LWL sows (1180 ± 81 vs. 702 ± 81 µmol/l, respectively, P = 0.01). Average NEFA concentration during lactation tended to be higher in HWL sows compared with LWL sows (989 ± 75 vs. 816 ± 67 µmol/L, respectively, P = 0.10) and was positively correlated with NEFA during gestation (r = 0.51, n = 27, P = 0.007). Leptin concentrations were similar between HWL and LWL sows during lactation (Table 3.1).
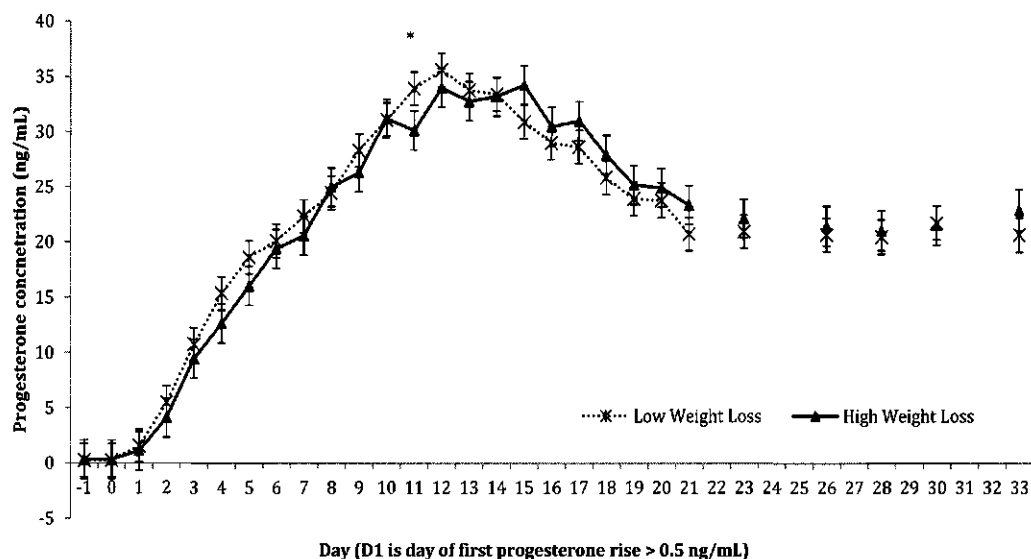
Figure 3.1 Progesterone profiles from d -1 to 33 after first rise of progesterone above 0.5 ng/mL for sows with a low (<13.77 %) or high (> 13.77%) lactation weight loss. * is a tendency (P < 0.1).

Plasma Urea profiles were similar for HWL and LWL sows (Figure 3.2C). Urea concentration on d 4 after weaning was lower in HWL than in LWL sows (5.3 ± 0.2 vs. 6.3 ± 0.2 mmol/L, respectively, P = 0.006). Average urea concentration during lactation was similar for HWL and LWL sows (Table 3.1) and was positively correlated with urea during gestation (r = 0.67, P = 0.0001).
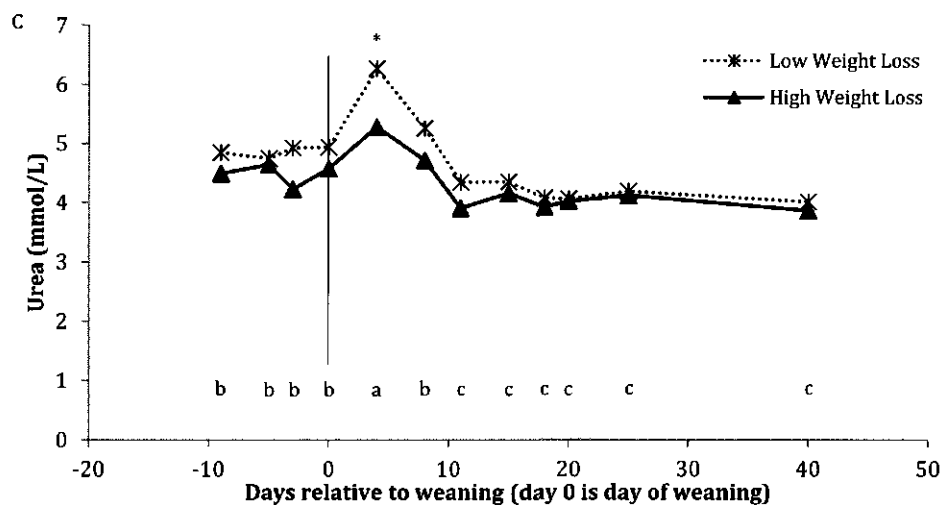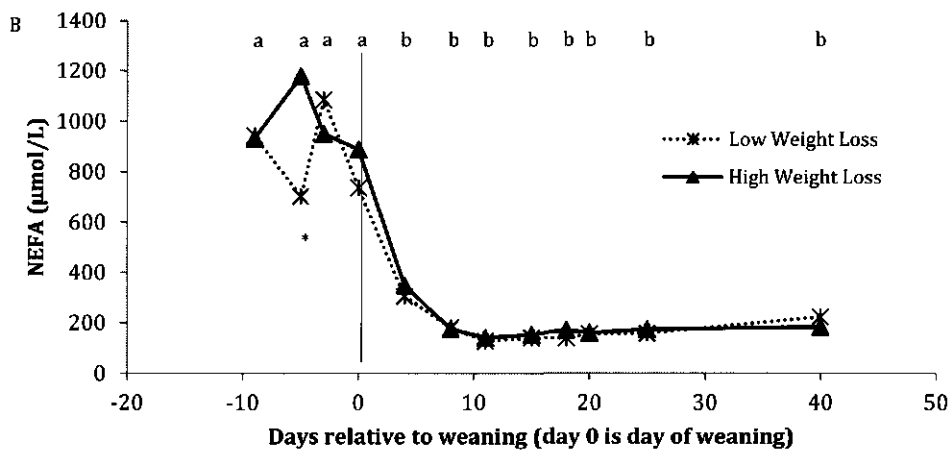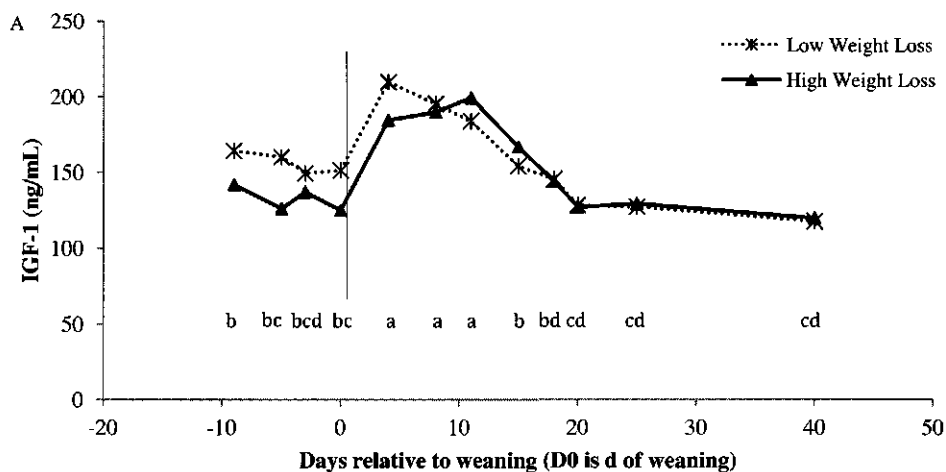
3.2.4 Correlations between metabolic parameters and metabolic parameters and reproduction
IGF-1 concentration during lactation was negatively correlated with weight loss (r = -0.38, p = 0.05) and relative weight loss during lactation (r = -0.33, P = 0.09). Furthermore, IGF-1 was negatively correlated with loin muscle loss (r = -0.48, P = 0.04) during lactation and tended to be positively correlated with back fat and loin muscle at weaning (respectively, r = 0.34, P = 0.08 and r = 0.41, P = 0.09).

NEFA concentration during lactation was negatively correlated with urea during lactation (r = -0.48, P = 0.01). Leptin concentration during lactation was positively correlated with NEFA concentration during lactation (r = 0.49, P = 0.009) and during gestation (r = 0.48, P = 0.001).

Figure 3.2 IGF-1 (A), NEFA (B) and Urea (C) profiles for sows with a low (<13.77%) or high (>13.77)
*lactation weight loss1 * Indicates significant difference between low and high weight loss sows*
1 SEM for low vs. high weight loss, respectively; 10.8 vs. 11.2 (IGF-1), 77.7 vs. 82.4 (NEFA), 0.2 vs. 0.2 (Urea)

Urea during lactation was negatively correlated with NEFA concentration during gestation (r = -0.41, P = 0.03) and tended to be negatively correlated with both back fat at farrowing and weaning (for both, r = -0.37, P = 0.06). Furthermore, urea concentration during lactation was negatively correlated with average progesterone concentration from d 1 to 10 and d 11 – 15 (r= -0.42, P = 0.03 and r=-0.52, P = 0.006, respectively), but not with other reproductive measures.

No significant correlations were found between plasma concentrations of IGF, NEFA, urea and leptin during either lactation or gestation or measures of reproductive performance on day 35 of gestation.

4 DISCUSSION

In the current study, sows with a high relative weight loss (>13.8%) during lactation had a lower embryonic survival rate and tended to have lower embryo numbers on day 35 of second gestation than sows with a low weight loss (≤13.8%) during lactation. Similar results are reported by authors who imposed feed or protein restriction, and thereby induced weight loss, in lactating primiparous sows (Baidoo et al., 1992b; Vinsky et al., 2006). In modern sows, feed restriction mainly affects embryonic survival or ovulation rate rather than weaning to oestrus interval (reviewed by Quesnel, 2009)). Genetic selection for short WOI, has led to sows that show oestrus shortly after weaning, but in which reproductive processes have not fully recovered from lactation (Quesnel, 2009). Contrarily, a recent study by Patterson et al. (2011) did not find effects of restricted feeding, 60% vs. 90% of calculated expected feed intake, on embryonic survival (70.3 vs. 71.2%, respectively) or number of live embryos (14.2 vs. 13.8, respectively) around day 28 of second gestation. In their study, feed restriction was applied during the last week of a 20 day lactation and resulted in 10% and 4% lactation weight loss for, respectively, feed restricted and control sows. The 10% weight loss might not have been severe enough to exert negative effects on embryonic survival. In our study, high weight loss sows lost on average 17.6% of their initial body weight at farrowing compared with an average loss of 11% in low weight loss sows, which resulted in a lower embryonic survival (-12%) at day 35 for the high weight loss sows. Even though embryonic survival and number of embryos were not affected by feed restriction in the study by Patterson et al. (2011), embryonic weight was significantly lower in their restrictedly fed sows compared with control sows (1.46 vs. 1.56 g, respectively, P < 0.03). Similarly, our study showed a tendency (P = 0.09) for lower embryonic weights in HWL compared with LWL sows.

In the current study, differences in embryonic survival between HWL and LWL sows were already present around implantation. The lower number of implantations can be caused by a lower ovulation rate or fertilization rate or a lower embryonic survival. In our study, ovulation rate was not different between HWL and LWL sows. Since oestrus duration and number of inseminations were similar between HWL and LWL sows, we do not expect

a different fertilization rate in both groups either. Embryonic survival is influenced by embryonic quality and uterine quality, but also by a synchronic development of embryos and uterus (Pope, 1988). Progesterone has a large influence on (synchronic) development of uterus and embryos, which is necessary for successful attachment starting after day 12 of gestation (Pope, 1988; Ashworth, 1992). In the current study, progesterone peak values were reached 1.4 days later in HWL than in LWL sows. The slower progesterone rise in HWL sows might have altered uterine secretions supporting embryonic development and could thereby have impaired development of the lesser developed embryos which could have decreased the number of implantations (Foxcroft, 1997). In addition, the lower embryonic survival and the lower weights of the embryos could be due to an impaired embryonic quality caused by the metabolic and hormonal alterations in sows in an catabolic state, as proposed by Paterson et al. (2011).

In the current study, IGF-1, NEFA, urea and leptin concentrations were measured during lactation to assess possible mechanisms by which lactation weight loss can affect reproductive performance. However, their concentrations were not statistically different between high and low weight loss sows, nor were they directly related to reproductive performance. Several studies, however, have shown that IGF-1 concentrations are related to follicle development (reviewed by Quesnel, 2009). In the current study, IGF-1 concentrations during lactation were numerically lower in HWL than in LWL sows. When IGF-1 concentrations were classified as low or high, regardless of sow weight loss, sows with a high IGF-1 concentration showed a tendency for a higher embryonic survival (results not shown).

In cows, high NEFA concentrations have been related to reduced embryonic development, either by affecting follicle or oocyte development before insemination or by acting on the uterine environment after insemination, or both (Leroy, 2005). In the current study, higher NEFA concentrations in HWL compared with LWL sows, may have compromised oocyte quality and thereby have affected embryonic survival, as has been reported for cattle. Leptin concentration during lactation was not different between HWL and LWL sows, which is in agreement with studies in primiparous sows (Mejia-Guadarrama et al., 2002).

Plasma urea concentration can reflect the protein intake in animals (Mejia-Guadarrama et al., 2002) and high urea concentrations (>10 ng/mL) indicate amino acid catabolism (Kraetzl et al., 1998). In the current study, urea concentrations were numerically higher in LWL compared with HWL sows. This may be a reflection of higher protein intake (Mejia-Guadarrama et al., 2002) which seems to correspond with the fact that fewer LWL sows had feed refusals during lactation (45% vs. 78%). Relations of urea concentration and reproductive performance have not been clearly established in pigs. In the current study, urea concentration during lactation was negatively correlated with progesterone concentrations at day 1-10 and d 11-15 of gestation, however, no clear mechanism can be found for this relation.
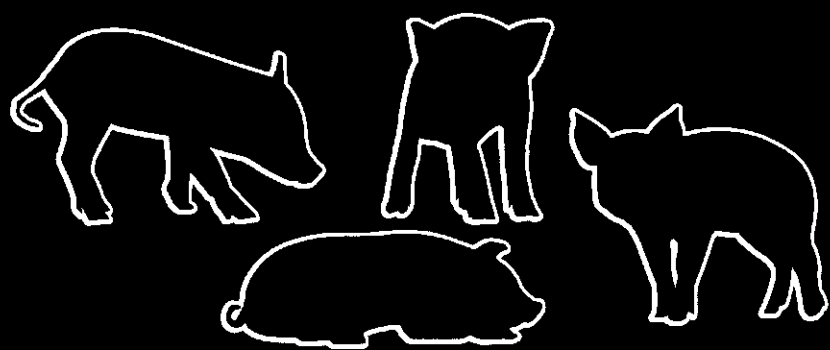
After weaning, sows quickly change from a catabolic to an anabolic state, as is indicated by the post-weaning drop of NEFA concentrations and rise of IGF-1 in both HWL and LWL sows, similar results are reported by Mejia-Guadarrama et al. (2002). The post weaning rise in urea indicates a surplus of nitrogen in both groups, probably because milk production has ceased and mammary glands regress. On d 4 after weaning, urea was significantly higher for LWL than HWL sows, indicating a nitrogen surplus in LWL sows. HWL sows, which lost more weight, might have used feed available nitrogen to restore their body reserves (Dourmad et al., 1996), whilst the need for restoration was lower in LWL sows. Average IGF-1, NEFA and urea concentrations during gestation (≥ day 8 after weaning) were not different between high and low weight loss sows and no direct relations between the gestation metabolic parameters and reproductive performance at day 35 of gestation were found.

Lactation weight loss is determined by the gap between energy output (maintenance plus milk yield or piglet growth) and energy input (feed intake). In the current study, litter weight was determined as a measure of energy output. Part of the higher weight loss in HWL sows can be explained by the extra milk production of these sows, resulting in a 4 kg higher litter weight at weaning compared with LWL sows. Unfortunately, even though feed refusals were weighed, dry matter was not assessed. We therefore only have an indication of actual feed intake. Nevertheless, a higher percentage of HWL sows had at least one feed refusal of more than 1 kg (wet weight) during the last two weeks of lactation compared with LWL sows (78% vs. 45%). These results seem to show that both a higher milk production and, possibly, a lower voluntary feed intake are causes of the higher weight loss in HWL sows.

Concluding, results from the current study show that high lactational weight losses negatively influence embryonic survival in mildly restricted sows. This negative effect is only mildly related to metabolic alterations during lactation and not with metabolic alterations during subsequent gestation. However, no (new) insight(s) in possible mechanisms explaining these differences were found. In addition, results showed that metabolic differences between HWL and LWL sows during lactation and weaning to insemination interval are not continued into gestation.
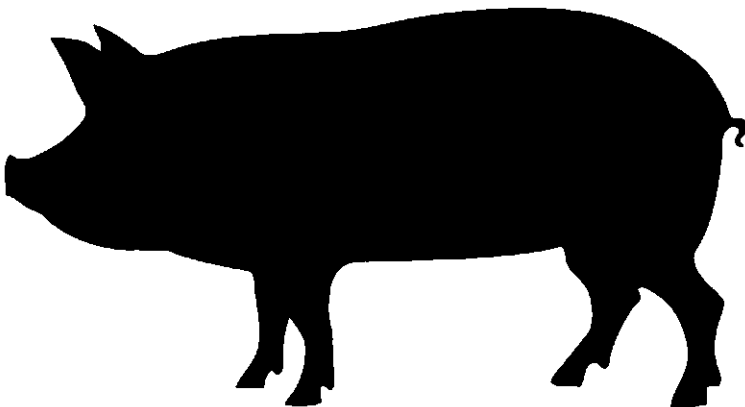
Acknowledgements

Chapter 4

Reproductive performance of second parity sows: Relations with subsequent reproduction

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Reproductive performance of second parity sows:
Relations with subsequent reproduction

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ABSTRACT

The objective of this study was to determine relations between reproductive performance, i.e. being a repeat breeder and litter size, in second parity and reproductive performance in later parities. In addition, relations between the first and second parity litter size and litter size in later parities were determined. First, 184,135 records from 46,571 sows were used to analyze the effect of being a repeat breeder in second parity on subsequent farrowing rate, litter size and parity number at culling. Second, 161,521 records of 39,654 sows were used to analyze the effect of litter size from first insemination in second parity, being either low (≤ 10 piglets total born), medium (11–13) or high (≥ 14), on subsequent litter size, farrowing rate and parity number at culling, with litter size in first parity included in the model as well. In total 15.7% of the sows inseminated in second parity were a repeat breeder in second parity. Being a repeat breeder in second parity did not affect litter size in subsequent parities, however it decreased farrowing rate in parity 3 (4.1%) and 4 (3.4%), but not in later parities ($P < 0.05$). Repeat breeders in second parity were culled on average 2 parities earlier compared with non-repeat breeders (resp. parity 5 vs. 7, $P < 0.05$). Sows with a low litter size in second parity showed a lower litter size in parity 3 and up compared with sows with a medium or high litter size in second parity ($P < 0.05$). The magnitude of this effect, however, decreased if litter size in first parity increased. For example, the difference in piglets born in parity 3–5 between sows with a low and high litter size in second parity was −4.6 piglets for sows with a low litter size in first parity. This difference decreased to −3.3 piglets for sows with a high litter size in first parity. Sows with a high litter size in second parity had 2% lower farrowing rate in parity 3, but not in later parities. Sows with a low litter size in second parity were culled 1 parity earlier compared with sows with a medium or high litter size in second parity. This study showed that a large part of the sows with poor reproductive performance in second parity can be expected to have a poor reproductive performance in subsequent parities. The effect of second parity litter size on subsequent litter size, however, depends on first parity litter size.

Keywords: Farrowing Rate, Litter Size, Subsequent, Reproductive Performance, Pigs

1. INTRODUCTION

Several papers addressed parity influences on reproductive performance, farrowing rate as well as litter size (e.g. Koketsu et al., 1999; Tummaruk et al., 2000; Hughes and Varley, 2003). Generally, reproductive performance increases with increasing parity number, reaching the highest level at parity 3 to 5, where parity changes at weaning. Second parity sows, i.e. sows of which their first litter is weaned, often have lower farrowing rates and/or smaller litter sizes compared with first parity sows (Penny et al., 1971; Morrow et al., 1989; Morrow et al., 1992; Saito et al., 2010) The major cause of poor reproductive performance of second parity sows seems to be insufficient development of the sow until onset of first lactation (Clowes et al., 2003b) or weight loss during this first lactation (Thaker and Bilkei, 2005). Lactational weight loss, induced by restricted feed or protein intake, during (parts of) first lactation has been demonstrated to have negative effects on follicle development at weaning and therefore on subsequent ovulation rate and embryonic survival which, in turn, can reduce farrowing rate and litter size (Clowes et al., 2003a; Prunier et al., 2003).
A reduction in reproductive efficiency of second parity sows might also decrease sow longevity, as culling rates increase with decreasing reproductive performance (Sasaki and Koketsu, 2008). Lucia et al. (2000) reported that reproductive failure is the main reason for culling in young sows. More recently, Saito et al. (2010) reported that sows with a lower litter size in second vs. first parity had a 1.2% higher culling risk compared with sows with a higher litter size in second vs. first parity. Effects of poor reproductive performance in second parity on reproductive performance in subsequent parities have been poorly described. Some indications for long-term effects of impaired reproduction in early parity are provided by Tummaruk et al. (2001b), who showed that re-breeders, in general, have a higher rebreeding risk in subsequent parities.
Thus, despite the fact that reproductive performance of second parity sows is often negatively affected, for example by lactation weight loss, and therefore lower than in first parity sows, relations with subsequent reproductive performance have not been documented. The objective of this study therefore is to determine relations between reproductive performance in second parity on farrowing rate, litter size and risk of culling in subsequent parities. In addition, relations between first and second parity litter size and litter size in later parities were determined.

2 MATERIALS AND METHODS

2.1. General

Data from 2000 to 2008 were available from Dutch sow farms that use the sow management program 'Farm' (Agrovision BV., Deventer, The Netherlands). Data on weaning to insemination interval, (re)breeding date, farrowing date and litter size (born alive, born dead) was available per parity for individual sows. If culled, parity number at culling was

available. Parity number changed at weaning and was used as follows, parity 1 is a gilt until the end of first lactation, parity 2 is a sow of which her first litter is weaned, parity 3 is a sow of which her second litter is weaned, etc. In total, 193,506 records of 48,212 sows from 87 Dutch farms were available. The 87 farms represent 6% of the sow herds in The Netherlands. The median herd size was 293, varying between 55 and 3200, which is slightly larger compared with the average in The Netherlands (265 sows, Bedrijfsvergelijking Agrovision B.V., Deventer, The Netherlands). These data were used to analyze the effect of being a repeat breeder in second parity on farrowing rate, litter size and culling in parity 3 and higher, and to analyze the effect of having a low litter size in second parity on farrowing rate, litter size and culling in parity 3 and higher.

To account for recording errors and to ensure data were valid and within normal physiological ranges, records were excluded if these did not meet the following criteria: age at first insemination between 160 and 400 days (median[1] 245 days), pregnancy length between 100 and 120 days (median 115 days), at least 1 piglet born alive (mean 11.5 piglet), lactation length between 10 and 41 days (mean 26.1 days) and weaning to first insemination interval between 0 and 35 days (median 5 days). To ensure all inseminated sows had a chance to farrow, sows with an insemination date of less than 120 days before the last farrowing date recorded on the farm were excluded. In total, 184,135 records of 46,571 sows from 87 farms remained available for analysis. This dataset will be referred to as 'FARROWING'. Only litter size from first insemination was used for analyses on litter size in third and higher parities, since prolonged intervals between weaning and conception in repeat breeders can positively influence litter size and thus be a confounding factor (Tummaruk et al., 2001b). Repeat breeders were therefore excluded from the data used for the analysis on litter size. This resulted in 161,512 records of 39,654 sows from 87 farms. This dataset will be referred to as 'LITTER'.

2.2. Repeat breeders, farrowing rate and litter size

A sow was considered a repeat breeder (RB) when she did not farrow from first insemination after weaning and received more than 2 inseminations, more than 5 days apart, within 1 parity. Regardless of being a repeat breeder, a sow was considered to have farrowed if she produced a litter after insemination. Farrowing rate from first insemination was defined as the proportion of sows that farrowed from first insemination after weaning. Farrowing rate of repeat breeders was calculated by dividing the number of repeat breeders that farrowed by the total number of repeat breeders. Sows that did not farrow after insemination were considered culled. Litter size is defined as the total number of piglets born (alive and dead), mummies not included. Litter size from first insemination is defined as the total number of piglets born from first insemination after weaning, i.e. excluding sows that return to estrus after first insemination after weaning.

2.2.1. Statistical analysis

Since multiple observations per farm and per sow cannot be regarded as independent units

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[1]Median was used if variable was not normally distributed

of observation, farm should be added to the statistical models as a random effect and sow as repeated measures effect; resulting in a multilevel model. However, due to the large number of data, there were computational limitations; sow effect could not be included in the models as a repeated measure, even if a random farm effect was not in the model. To study the effect of multilevel repeated and random effects without having computational restrictions, analysis was done on a randomly selected 35% of the data (n=60,000; proc Survey select, SAS, SAS Inst. Inc., Cary, NC, USA) in which multilevel analysis could be performed. Analysis on five different random selections with farm and sow effect included, showed that repeated sow effect explained between 3.5 and 3.8% of the total unexplained variance. Farm effect explained between 4.5 and 5.1%. As the repeated effect of sow was smaller than random herd effect, and a part of the variation due to sows is already included as sow level explanatory variables in the statistical models, whilst herd level explanatory variables were not available and sow effect not within computational limits when analyzing the complete dataset, we decided to only include farm as random effect in the analysis of the whole dataset. Moreover, some of the remaining variation due to sows within herds is then included in the random herd effect. This is further justified by the fact that both effects explain only a small percentage. A random farm effect was added to the models described below, using a compound symmetry covariance structure. Furthermore, year was added to the models as a random effect to account for increased genetic potential for litter size over the years studied. The proportion of unexplained variance due to year was only 0.005 and therefore results per year were not included in the Results section.

2.3. Farrowing

Farrowing (yes/no), from parity 3 and up was analyzed as a dichotomous outcome variable using generalized linear regression with a binomial distribution and a log-link function (proc Glimmix, SAS). For effect of being a repeat breeder on farrowing rate, the dataset 'FARROWING' was used with the explanatory variables parity (1, 2, 3, 4, 5, 6, 7 and ≥8), being a repeat breeder in second parity (RB yes/no) and their interaction as fixed effects in the model. For effect of litter size in second parity on farrowing rate, the dataset 'FARROWING' was used with the explanatory variables parity, litter size in second parity (low, medium, high, see next paragraph) and their interaction as fixed effects in the model.

2.4. Litter size

Litter size in parity 3 and up and the sum of litter sizes in parity 3–5 were both analyzed as a continuous outcome variable using a generalized linear model (proc Mixed, SAS). Assumptions of normality were checked by examining model residuals. Residuals were assumed to be normally distributed when skewness and kurtosis had values between –2 and 2. For these analyses, the dataset 'LITTER' was used. As litter size in first and second

parity, as explanatory variables, were not linearly related with the outcome variables, they were classified as low (L), medium (M) or high (H), based on the average litter size of first (11.4±0.01) and second (12.0±0.02) parity. Litter size in first parity was classified as: ≤10 piglets (1 L, 37%), 11 or 12 piglets (1M, 27%) and≥13 piglets (1 H, 36%). Since litter size in first parity was 11.4 we classified the medium litter size as 11 or 12 piglets total born (27% of the sows). Litter size in second parity was classified as: ≤10 (2 L, 30%), 11 to 13 (2M, 37%) and ≥14 piglets (2 H, 33%), since 12.0 was the average litter size in second parity.

In the model for the analysis of the effect of litter size in second parity on litter size in parity 3 and up, the explanatory variables parity (1, 2, 3, 4, 5, 6, 7 and ≥8), litter size in first parity (1L, 1M, 1H), litter size in second parity (2L, 2M, 2H) and their interactions were included in the model for parity 3 and up as fixed effects. For effect of being a repeat breeder in second parity on litter size in parity 3 and up, the dataset 'FARROWING' was used with the explanatory variables parity, being a repeat breeder in second parity (RB yes/no) and their interaction as fixed effects in the model. For this analysis repeat breeders in parity 3 and up were excluded.

In the model for the analysis of sum of litter size in parity 3–5, litter size in both first and second parity and their interaction were included in the model. The analysis on sum of litter size of parity 3–5 was done in order to compare the effect of first and second parity litter sizes for sows that were not culled until 5th parity (30% of total), since culling may be associated with lower litter size in older parities.

Values presented are least squares means with their standard error (SEM), corrected for the variables in the model.

2.5. Culling

Culling was studied by using non-parametric survival analysis (proc Lifetest, SAS Inst. Inc., 2004). For 'FARROWING', Kaplan–Meier survivor functions were estimated for both repeat and non-repeat breeders and compared using the log-rank test. For 'LITTER' survivor functions of Low, Medium, and High litter sizes in second parity were compared. Values presented are the medians of parity of culling for the different survivor functions. Since reasons for culling were not reported, inferences on reasons for culling could not be tested statistically.

3. RESULTS

3.1. Descriptive statistics

Table 4.1 shows reproduction characteristics for datasets 'Farrow' and 'Litter'. Farrowing rate from first insemination was 84.2% for 'Farrow' and 100% for 'Litter', the latter due to exclusion of repeat breeders and sows that did not farrow. For both datasets mean parity number (±std) was 3.4 ± 2.3 and mean litter size (±std) was 12.3 ± 3.3 piglets.

Farrowing rate from first insemination was lowest in second parity sows (79.9%) and highest in parity 3 and up (85.2%); farrowing rate from first insemination in first parity sows was in between (81.2%, $P < 0.05$; Table 4.2). Repeat breeders had a lower farrowing rate compared to non-repeat breeders ($P < 0.05$). The differences were 7.3%, 1.1%, and 12.4% for respectively first, second and parity 3 and up, with the smallest difference in second parity sows (Table 4.2).

Litter size from first insemination increased from first to second to third parity and up (from 10.8 to 11.4 to 12.2 piglets; $P < 0.05$). Repeat breeders had a higher litter size compared to non-repeat breeders in first and second parity (resp. 0.3 and 0.7 piglet; $P < 0.05$, Table 4.2), but not in parity 3 and up. Average litter size was 8.2 ± 0.02 for 1L, 11.5 ± 0.02 for 1M and 14.3 ± 0.02 piglets for 1H ($P < 0.05$). Average litter size was 8.1 ± 0.02 for 2L, 12.0 ± 0.02 for 2M and 15.5 ± 0.02 piglets for 2H ($P < 0.05$).

3.2. Effects of being a repeat breeder in second parity (RB)

3.2.1. On farrowing rate
In total, 15.7% of the sows inseminated in second parity was a repeat breeder (RB) (Table 4.2). Farrowing rate for second parity RB sows was 4.1% lower in 3rd parity and 3.4% lower in 4th parity compared to non-RB ($P < 0.05$, Fig. 4.1). In 5th and later parities, farrowing rate was not significantly affected by rebreeding in second parity ($P < 0.05$; P-interaction < 0.05, Fig. 4.1).

3.2.2. On litter size in parity 3 and up and sum of litter size in parity 3–5
Being a repeat breeder in second parity did not affect litter size in parity 3 and up or sum of litter size in parity 3–5 ($P < 0.05$; P-interaction < 0.05).

3.2.3. On parity of culling
RB sows were culled 2 parities earlier (median parity of culling = 5) compared to non-RB sows (median parity of culling = 7, $P < 0.05$).

Table 4.1 Reproduction characteristics for datasets 'Farrow' and 'Litter'

Dataset		Farrow		Litter*	
Variable	Class	Mean	STD	Mean	STD
Repeat breeders (%)		12.3		0.0	
Lactation Length (days)		26.1	4.4	26.1	4.1
Weaning to estrus interval (days)		6.2	4.5	6.1	4.3
Repeat breeder in 2nd parity (%)		15.7		10.0	
Litter Size class 2nd parity (%)	Low	30.0		30.0	
	Medium	36.0		37.0	
	High	34.0		33.0	
Sows per parity class (%)	1	25.3		24.6	
	2	20.1		19.3	
	3	15.5		15.8	
	4	11.9		12.2	
	5	9.1		9.5	
	6	6.8		7.1	
	7	4.8		4.9	
	≥8	6.5		3.8	

* Only data from first insemination

Table 4.2 Reproduction characteristics of sows in first, second and third parity and up

Parity	1st	2nd	3rd
No. of cycles at 1st insemination	42,828	33,064	91,083
Overall farrowing rate (%)*	92.0^a	92.2^a	93.3^b
Overall Litter Size# (n)	11.0 (0.13)^a	11.8 (0.13)^b	12.2 (0.13)^c
Farrowing rate 1st insemination (%)	81.2^{ax}	79.9^{bx}	85.2^{cx}
Litter size from 1st insemination# (n)	10.8 (0.13)^{ax}	11.4 (0.13)^{bx}	12.2 (0.13)^c
Repeat breeders (%)	14.0	15.7	9.9
Farrowing rate repeat breeders (%)	73.9^y	78.8^y	72.8^y
Litter size repeat breeders (n)#	11.1 (0.14)^{ay}	12.1 (0.14)^{by}	12.2 (0.15)^b

* Indicates those sows that produced a litter after insemination; other sows were culled

lsmeans (SEM)

^{abc} different superscripts within rows indicates significant difference (P < 0.05) between parities, after correction for farm (random effect)

^{xyz} different superscripts within columns indicates significant difference (P < 0.05) between the results from 1st insemination and repeat breeders, after correction for farm (random effect)
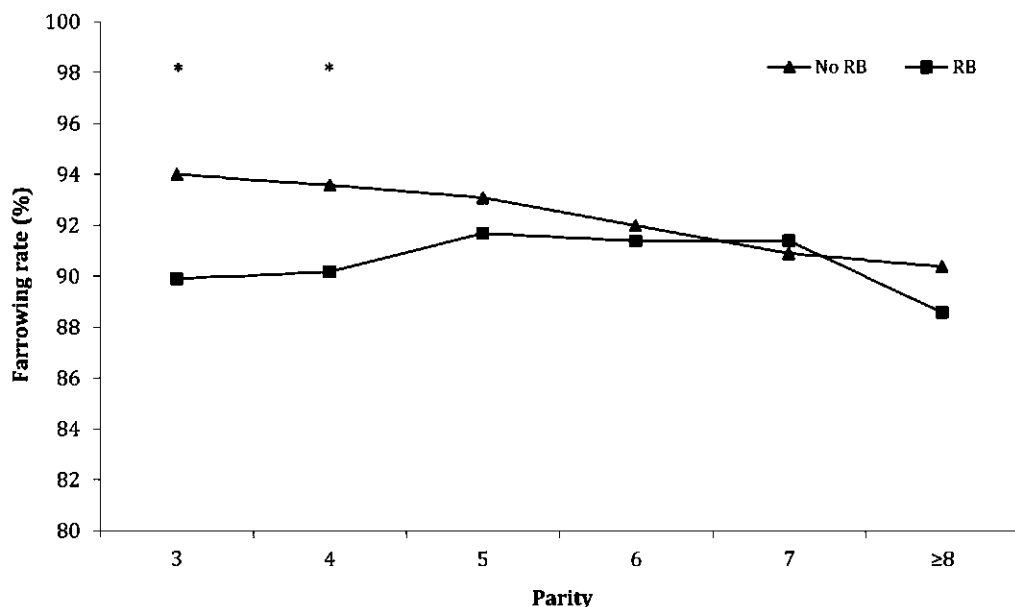
*Figure 4.1 Farrowing rate per parity for sows that were (RB) or were not (No RB) a repeat breeder in 2nd parity. * indicates a significant difference (P<0.05) within parity (corrected for random farm effect)*

3.3. Effects of litter size in second parity

3.3.1. On farrowing rate

Farrowing rate in 3rd parity was 2% lower for 2L compared with 2M and 2H sows (resp. 92.6% vs. 94.6% and 94.6%, P< 0.05, P-interaction < 0.05). For other parities, farrowing rate was not different between 2H, 2M and 2L sows.

3.3.2 On litter size in parity 3 and higher.

Fig. 4.2 shows the relation between litter size classes in first and second parity and the lsmeans (±sem) of litter size in parity 3 and up. Litter size in parity 3 and up decreases with both decreasing first and second parity litter size (Fig. 4.2a–c), though not independently (P-interaction < 0.05). Results show that when litter size in second parity is lower, litter size in parity 3 and up is lower as well. However, the size of the effect is dependent on the litter size class in first parity. For sows with a low first parity litter size (1L, see Fig. 4.2a), second parity litter size categories had a large influence on litter size in 3rd and higher parities, whereas for sows with a high first parity litter size (1H, see Fig. 4.2c), effects of second parity litter size on litter size in parity 3 and up were smaller. For example, for 1L sows there was a 0.6 piglet difference in litter size in 3rd parity between sows with a low litter size in second parity (2L) and sows with a medium litter size in second parity (2M; Fig. 4.2a), whilst the difference in 3rd parity litter size between 2L and 2M was only 0.2 piglet for sows with a high first parity litter size (Fig. 4.2c). If second parity litter size

was high, there was no difference between 1L and 1M sows (upper line in Fig. 4.2a vs. upper line in Fig. 4.2b). However, sows with a high litter size in both first and second parity gave the highest litter sizes in parity 3 and up.

3.3.3. On sum of litter size in parity 3-5

Table 4.3 shows the first and second parity litter sizes per class, as well as the sum of the 3rd to 5th parity litter sizes per class for sows that were not culled between parity 1 to 5. Although based on only 30% of the sows that were present at first parity, these results are similar (Table 4.3) as compared to analyses on litter size in parity 3 and higher (as shown separately in Fig. 4.2). Regardless of litter size in first parity, sows with a high litter size in second parity produced more piglets from parity 3 to 5 than sows with a low litter size in second parity (4.6, 3.7 and 3.3 piglets for 1L, 1M and 1H, respectively). Similarly to the analyses on litter size parity 3 and higher, the size of the effect decreased with increasing litter size in parity 1 (interaction $P < 0.05$).

3.3.4. On parity of culling

Sows with a low litter size in second parity (2L) were culled at an earlier parity (median parity of 6) compared to sows with a medium (2M) or high litter size in second parity (2H) (median parity of 7; $P < 0.05$).

Table 4.3 Average litter size (lsmeans (SEM)) in first, second and 3rd-5th parity for sows in Low, Medium and High litter size classes in first and second parity[1] and the total number of sows (N) per group

1st parity litter size class	2nd parity litter size class	Litter size (lsmean (se))			N (% per 1st parity group)
		1st parity	2nd parity	3rd - 5th parity	
Low (1L)	Low (2L)	8.2 (0.02)	8.2 (0.02)	34.2 (0.4)^{cy}	10,494 (37.0%)
	Medium (2M)	8.3 (0.03)	11.9 (0.02)	35.7 (0.4)^{cy}	11,619 (41.0%)
	High (2H)	8.2 (0.02)	15.3 (0.02)	38.8 (0.4)^{bx}	6,203 (22.0%)
Medium (1M)	Low (2L)	11.5 (0.03)	8.3 (0.02)	35.4 (0.4)^{by}	7,255 (29.2%)
	Medium (2M)	11.5 (0.02)	12.0 (0.02)	36.8 (0.4)^{by}	10,146 (40.8%)
	High (2H)	11.5 (0.03)	15.3 (0.02)	39.1 (0.4)^{bx}	7,471 (30.0%)
High (1H)	Low (2L)	14.1 (0.03)	8.1 (0.02)	37.5 (0.4)^{ay}	6,053 (18.7%)
	Medium (2M)	14.2 (0.03)	12.1 (0.02)	38.1 (0.4)^{ay}	11,112 (34.3%)
	High (2H)	14.6 (0.03)	15.7 (0.02)	40.8 (0.4)^{ax}	15,186 (47.0%)

[1] 1st parity classes: Low (≤10 piglets), Medium (11-12 piglets) and High (≥13 piglets) and 2nd parity classes Low (≤10 piglets), Medium (11-13 piglets) and High (≥14 piglets)

[abc] significant difference of litter size between 1st parity litter size classes within 2nd parity litter size class

[xyz] significant difference of litter size in parity 3-5 ($P < 0.05$) between 2nd parity litter size classes within 1st parity litter size class
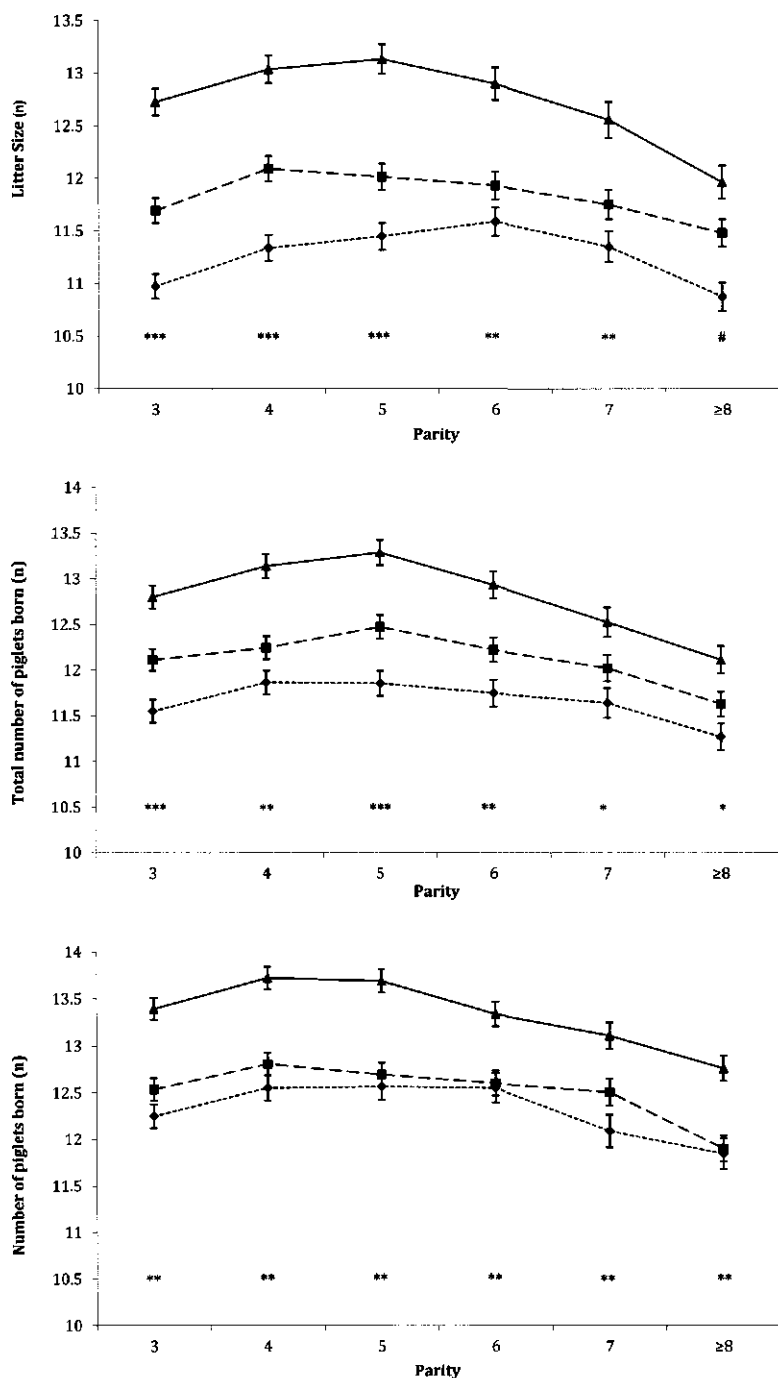
Figure 4.2 Litter size (lsmeans±sem) in 3rd and higher parities for sows with a Low (1L: ≤10, 2a), Medium (1M: 11-12, 2b) or High (1H: ≥13, 2c) litter size in 1st parity, subdivided in sows with a Low (2L: ≤10, dotted line), Medium (2M: 11-13, dashed line) or High (2H: ≥14, solid line) litter size in 2nd parity.

***   *indicates significant difference (P<0.05) between 2H and 2M and 2L (corrected for random farm effect)*
**   *indicates significant difference (P<0.05) between 2H and 2M or 2L (corrected for random farm effect)*
#   *indicates significant difference (P<0.05) between 2L and 2M or 2H (corrected for random farm effect)*
*   *indicates significant difference (P<0.05) between 2H and 2L (corrected for random farm effect)*

4. DISCUSSION

The main aim of this study was to relate reproductive performance of second parity sows with farrowing rates and litter sizes in subsequent parities and parity at culling. Results showed that a low litter size in second parity and being a repeat breeder in second parity were indeed associated with lower subsequent reproductive performance and a lower parity at culling. Therefore, subsequent performance is lower for sows with poor reproductive performance in second parity. The mechanisms by which subsequent reproductive performance is influenced seem to be different for being a repeat breeder in second parity and for having lower litter size in second parity, as is indicated by the fact that being a repeat breeder in second parity was not associated with litter size in subsequent parities and litter size in second parity was not associated with farrowing rate in subsequent parities. The studied farms represent 6% of all Dutch sow farms and were randomly selected from farm using the sow management program 'Farm' (20% of all farms using sow management programs). Average herd size was slightly larger compared with the Dutch average (293 vs. 265 sows), whilst litter size (total born) was 0.7 piglet lower (12.3 vs. 13.0). The latter, however, may partly be related to the lower average parity number in our dataset compared with the Dutch average (3.4 vs. 4.1), since litter size increases from parity 3 to 6 (Hughes and Varley, 2003). In total 5% of the original data were not used because they did not meet our inclusion criteria. These criteria were based on normal ranges for the studied parameters. These 5% may reflect (possible) recording errors. One can still debate if a gestation length between 100 and 108 days (0.17% of the remaining data), a lactation length of 10–17 days (1.5% of the remaining data) or a weaning to insemination interval of 0 or 1 day (0.5% of the remaining data) are within normal ranges. However, since sows with these characteristics will be inseminated in practice, and since they only represent a small proportion of the data we decided not to exclude them from the analysis.

4.1. Litter size in second parity

Litter size in second parity was related with litter size in subsequent parities. Litter size in 3rd parity and up was lower in sows with a low (≤10 piglets) litter size in second parity compared with sows with a medium (11–13 piglets) or high (≥14 piglets) litter size in second parity. This effect, however, was dependent on litter size in first parity. If litter size in first parity was high, effects of second litter size class were less pronounced. These effects were independent of potential effects of culling low performing sows, since similar effects were found for litter size in parity 3 and up (with decreasing number of sows due to culling) and summed litter size in parity 3–5 (only for sows that were culled after 5th parity). Litter size is determined by genetic potential as well as environmental factors such as management and climate. Genetic correlations of litter size between parities are relatively high. Hanenberg et al. (2001) reported a genetic correlation of 0.84 between litter size in first and second parity, whilst Oh et al. (2006) reported a genetic correlation

of 0.88 between litter size in first and older parities. A high genetic correlation means that a sow with a low or high litter size in first and second parity is expected to also have a, respectively low or high litter size in subsequent parities. In our study, sows with the lowest production in parity 3 and up were sows with a low litter size in first and second parity, which indeed may be the sows with a low genetic potential for litter size. Similarly, sows with the highest production in parity 3 and up also had a high litter size in first and second parity and may indeed be the sows with a high genetic potential for litter size.

A high genetic potential for litter size may imply that these sows have an advantage in reproductive physiology, i.e. high uterine capacity, but it may also imply that these sows are better able to withstand environmental factors, i.e. climate condition or nutritional state, affecting physiological factors. Despite high genetic correlations, phenotypic correlations for litter size between parities are relatively low (0.04: Hanenberg et al., 2001; 0.18: Oh et al., 2006; 0.24: this study). A low phenotypic correlation indicates a large environmental effect on, in this case, litter size. Data from our study show that sows with good performance in the first parity can have relatively poor performance in the second parity, which may be a result of environmental factors, e.g. severe weight loss during lactation (Thaker and Bilkei, 2005) or poor sow development during the first parity (Hoving et al., 2010). Similarly, sows with poor litter size in first parity can also have good performance in later parities. Poor litter size in first lactation may be due to environmental factors, such as poor insemination management or a higher embryonic mortality due to high feed intake in early pregnancy (Pharazyn, 1992; Jindal et al., 1996). A more recent study by Quesnel et al. (2010) shows no negative effect of feeding level on embryonic mortality. These authors, however, used highly prolific gilts that may have a different predisposition to embryonic mortality in relation with high feeding level during early pregnancy compared with the sows used in our data analysis.

An intriguing question is if poor reproduction in the first or second parity, due to improper management, may have lasting effects on subsequent reproduction. Data on this are very scarce. Morrow et al. (1990) studied effects of different management strategies, like skip a heat after first weaning, altrenogest supplementation after first weaning and split weaning during first lactation, in order to improve second parity litter size. Data show that e.g. skip a heat improves litter size in second parity and showed an numerically increase in litter size, of 0.8 pigs live born, in parity 3–6. Similarly, Vesseur (1997) found a numerically increase of 0.9 total born piglets in 3rd parity. In addition, Sasaki and Koketsu (2008) reported that in sows with a high lifetime efficiency and longevity, fewer sows had had a decrease in litter size between first and second parity compared with sows with a low lifetime efficiency and longevity. Our data also indicates tha - in general - sows with a poor litter size in the second parity remain poor performers in later parities. This effect is reduced in sows with a high first litter size, but not lost.
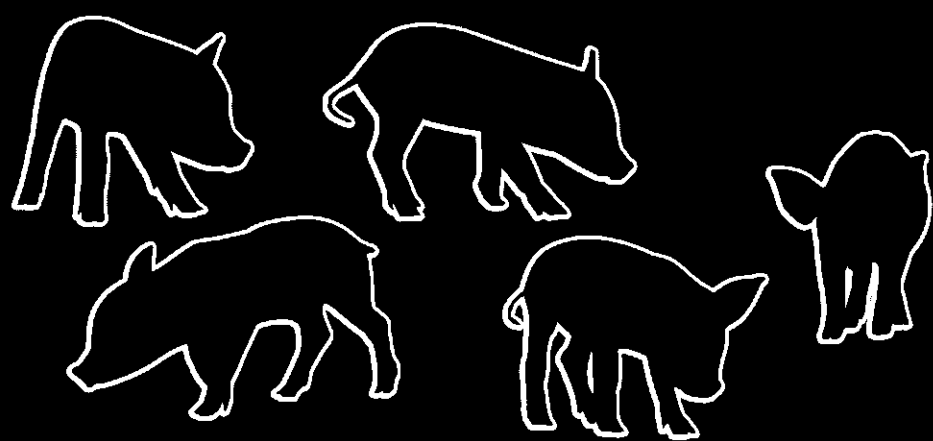
4.2. Being a repeat breeder in second parity

Of all sows inseminated in second parity, 15.7% became a repeat breeder. Being a repeat breeder in second parity was negatively associated with farrowing rate in 3rd (−4%) and 4th parity (−3%). Similarly, Koketsu (2003) reported that, on average, 35% of the sows that are re-serviced once, are re-serviced again in later parities. Tummaruk et al.(2001b) reported that if sows were a repeat breeder in first or second parity sows, farrowing rate tended to be lower in subsequent parities (1.3% for Landrace and 2.4% for Yorkshire sows). Perhaps sows that become a repeat breeder more than once have a different estrus duration or expression, which makes it more difficult to inseminate them at the right time (Koketsu, 2003). It is also possible that these sows are more sensitive to environmental influences that affect reproduction, such as stress during gestation (Einarsson et al., 2008; Ashworth et al., 2009), compared with sows that do not become repeat breeders.
Being a repeat breeder in second parity was not related with litter size in subsequent parities. Repeat breeders in second parity, however, were culled 2 parities earlier compared with non-repeat breeders. Koketsu et al. (1999) reported that repeat breeders in parity 1 are culled one parity younger compared to non-repeat breeders in parity 1. Culling due to non-pregnancy is the most common reason for culling in young sows (Lucia et al., 2000). Since the number of non-productive days is increased in sows that return to estrus, being a repeat breeder is an important selection criterion for sow farmers (Sasaki and Koketsu, 2008). The fact that repeat breeders in second parity were culled 2 parities earlier compared with non-repeat breeders whilst sows with a low litter size in second parity were culled only one parity earlier than sows with a medium or high litter size in second parity, indicates that being a repeat breeder is a more important reason for culling for sow farmers than having fewer piglets. Similarly, Sasaki and Koketsu (2008) reported that farmers might cull sooner for fertility traits (i.e. repeat breeders) than for litter size traits, since repeat breeders have more non-productive days compared with sows with lower litter sizes.

5. CONCLUSION

From this study we can conclude that sows with a poor reproductive performance in second parity, being a repeat breeder or having a low litter size, also have, respectively, poor farrowing rates and litter sizes in subsequent parities and are culled earlier compared with sows with an average or good reproductive performance. The magnitude of the effect of low litter size in second parity on subsequent reproductive performance is dependent on litter size in first parity. In order to understand the physiological background of these findings, more research is needed on long term effects of reproductive management in young sows.
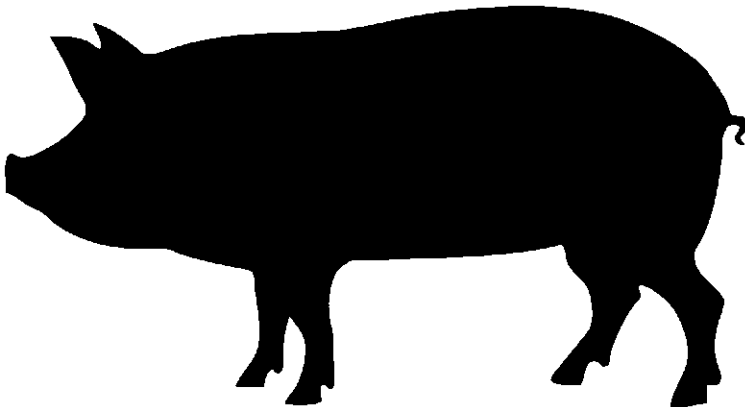
Chapter 5

An increased feed intake during early pregnancy improves sow bodyweight recovery and increases litter size in young sows

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E. A. M. Graat, H. Feitsma and B. Kemp

An increased feed intake during early pregnancy improves sow body weight recovery and increases litter size in young sows

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ABSTRACT

This study evaluated the effect of feeding level and protein content in feed in first- and second parity sows during the first month of gestation on sow body weight (BW) recovery, farrowing rate, and litter size during the first month of gestation. From days 3 to 32 after the first insemination, sows were fed either 2.5 kg/d of a standard gestation diet (control, n = 49), 3.25 kg/d (+30%) of a standard gestation diet (plus feed, n = 47), or 2.5 kg/d of a gestation diet with 30% greater ileal digestible amino acids (AA) (plus protein, n = 49). Feed intake during the experimental period was 29% greater for sows in the Plus Feed group compared with those in the Control and Plus Protein groups (93 vs. 72 kg, P < 0.05). Sows in the plus feed group gained 10 kg more BW during the experimental period compared with those in the control and plus protein groups (24.2 ± 1.2 vs. 15.5 ± 1.2 and 16.9 ± 1.2 kg, respectively, P < 0.001). Back fat gain and loin muscle depth gain were not affected by treatment (P = 0.56 and P = 0.37, respectively). Farrowing rate was smaller, although not significantly, for sows in the Plus Feed group compared with those in the Control and Plus Protein groups (76.6% vs. 89.8 and 89.8%, respectively, P = 0.16). Litter size, however, was larger for sows in the Plus Feed group (15.2 ± 0.5 total born) compared with those in the Control and Plus Protein groups (13.2 ± 0.4 and 13.6 ± 0.4 total born, respectively, P = 0.006). Piglet birth weight was not different among treatments (P = 0.65). For both first- and second- parity sows, the plus feed treatment showed similar effects on BW gain, farrowing rate, and litter size. In conclusion, an increased feed intake (+30%) during the first month of gestation improved sow BW recovery and increased litter size, but did not significantly affect farrowing rate in the subsequent parity. Feeding a 30% greater level of ileal digestible AA during the same period did not improve sow recovery or reproductive performance in the subsequent parity.

Key words: Feeding Level, Reproductive Performance, Sow Development

1.INTRODUCTION

Second parity sows often show a reduced farrowing rate, a reduced litter size, or both compared with first parity sows (Morrow et al., 1992; Hoving et al., 2010). This reduced reproduction in second parity is associated with negative energy balance (i.e., body weight loss) during the first lactation (Thaker and Bilkei, 2005). Several studies have reported that a lactational body weight (BW) loss of >10 to 12% decreases reproductive performance in the subsequent parity (Clowes et al., 2003a; Thaker and Bilkei, 2005). Of the different components of BW loss, protein loss seems to have the largest influence on subsequent reproduction (Clowes et al., 2003a;b; Willis et al., 2003). Early pregnancy may be the best period for a sow to recover from lactational losses (Dourmad et al., 1996). This period is especially important for young sows because they also need to grow to reach mature body size. In practice, however, young sows are often kept at restricted feeding levels during early pregnancy. This strategy mainly originates from studies in gilts, which show that increased feeding levels in early pregnancy increase embryonic mortality (Pharazyn, 1992; Jindal et al., 1996). There is, however, no evidence that this also holds for sows that need to recover from a previous lactation. Moreover, the negative effects of an increased feeding level during early gestation are questioned even in gilts, as is shown by Quesnel et al. (2010). The present study was performed to evaluate the effects of feeding level and protein content in the feed during the first 4 wk of gestation in first- and second-parity sows on sow body recovery (i.e., BW, back fat, and loin muscle depth) and subsequent farrowing rate and litter size.

2. MATERIALS AND METHODS

All experimental procedures were approved by the Institutional Animal Use and Care Committee of Wageningen University (Wageningen, the Netherlands).

2.1 Animals and Treatment

In total, 146 crossbred (Yorkshire × Dutch Landrace) first-parity (n = 101) and second-parity (n = 45) sows, inseminated between April 2008 and September 2009, were used. After insemination, sows were divided into 1 of 3 treatments per parity group (parity 1 or 2). The treatments were 1) control: 2.5 kg/d of a standard gestation diet (Table 5.1); 2) plus feed: 3.25 kg/day of the standard gestation diet; and 3) plus protein: 2.5 kg/day of a gestation diet with 30% greater ileal digestible AA. The latter was mainly established by adding extracted soybean meal to the diet at the expense of corn, barley, and wheat (Table 5.1). During the experiment, which lasted 16 months, the basic ingredients were analyzed every month. The total content of the feed was calculated monthly based on the analyses of the ingredients, resulting in the values (mean ± SD) presented in Table 5.1. Treatments were applied from days 3 to 32 after insemination.

2.2 Housing and Feeding

Preceding and during lactation and after treatment, sows were housed in farrowing crates (2.4 × 1.8 m), received a commercial lactation diet, and had ad libitum access to water. Within 3 days after farrowing, litters were standardized to 11 or 12 piglets. After weaning, sows were housed individually in crates (2.3 × 0.6 m) and were fed 3 kg/d of the commercial lactation diet divided over 2 portions (0800 and 1600 h). Sows were checked for estrus 2 times per day (0900 and 1530 h) using the back-pressure test in the presence of a mature teaser boar. Twenty-four hours after the first standing heat reflex, sows were inseminated with a commercial dose of semen (2×10^9 sperm cells of a Topigs boar line; Topigs, Vught, the Netherlands). If still in estrus, sows received a second insemination 16 to 24 h after the first insemination.

2.3 Gestation

About 3 days (2.8 ± 0.8 days) after the first insemination, sows were moved to the gestation room. During the following 30 days, sows were individually housed and received the feeding treatment. Sows were fed twice per day (0900 and 1600 h). From day 18 of gestation onward, sows were checked for signs of estrus twice daily using a mature teaser boar. Date of return to estrus after the first insemination was recorded as the first date a standing heat reflex was observed. Around 4 weeks of gestation, an ultrasound scan (MS Multiscan Digital, MS Schippers, Bladel, the Netherlands) was performed to confirm pregnancy. If an animal did not return to estrus but was diagnosed as not pregnant by ultrasound, the date of the ultrasound scan was recorded as the date when the sow was no longer pregnant. The feed level of sows in the Plus Feed group was decreased for 3 days (days 33 to 35) from 3.25 kg to the standard feeding level of 2.8 kg. After day 35 of gestation, the sows were housed in groups of 14 animals and received 2.8 kg of feed per day. The feeding level in the Control and Plus Protein groups was increased in 2 days from 2.5 to 2.8 kg of feed per day. During feeding, the sows were locked in the crates for 30 min to give each sow the chance to eat its portion of the feed. During the whole gestation period, water was available ad libitum.

2.4 Measurements

During the treatment period, feed refusals were collected daily and feed intake per sow was calculated on a weekly basis.

2.4.1 Sow Development.
Body weight, back fat, and loin muscle depth were measured the day after farrowing, preceding treatment, at weaning, at onset of the feeding treatment, at the end of the feeding treatment, and after farrowing, after treatment. Back fat was measured 6 cm above the midline, directly above the last rib on the left and right sides of the animal, using a

Renco Meter (MS Schippers). Loin muscle depth was measured at the same locations using an Aloka Ultrasound instrument (Aloka SSD-500, Biomedic Nederland BV, Almere, the Netherlands). For the loin muscle measurement, 2 measurements were made on both the left and right sides of the animal. If the 2 measurements at 1 side differed by more than 2 mm, a third measurement was made.

2.4.2 Reproduction.

Weaning-to-estrus interval and date and time of inseminations were recorded. Date of returning to estrus after insemination or date of farrowing, number of piglets born alive, and number of piglets born dead were recorded. In addition, piglet birth weights 24 h after birth and piglet mortality from days 1 to 3 after birth were recorded.

2.5 Statistical Analysis

Among the 146 inseminated sows, data from 1 pregnant sow from the control group that died shortly before farrowing was excluded from all analyses. Normality was checked by examining model residuals, with a skewness and kurtosis between −2 and 2 considered normal. Statistical differences before the treatment were determined using a general linear regression model (PROC GLM, SAS Inst. Inc., Cary, NC) with parity (1, 2), treatment (Control, Plus Feed en Plus Protein), and their interaction as fixed effects. Preliminary analyses showed that the interaction was never significant (P > 0.05). Therefore, it was excluded from the model. Farrowing rate was analyzed using logistic regression (PROC Logistic, SAS Inst. Inc.). The model included treatment (Control, Plus Feed en Plus Protein), parity (1, 2), and their interaction as fixed effects. Piglet mortality was analyzed using logistic regression (PROC Genmod, SAS Inst. Inc.). The model included treatment (Control, Plus Feed en Plus Protein), parity (1, 2), and their interaction as fixed effects, and sow as a repeated measure. An exchangeable correlation structure was used to account for within-sow variation. Data on litter size, piglet birth weight (of piglets born alive and dead), CV of piglet birth weight (CVpbw), sow body weight, backfat depth, and loin muscle depth were analyzed using general linear regression (PROC GLM; SAS Inst. Inc.). In all models, treatment (Control, Plus Feed, Plus Protein), parity (1, 2), and their interaction were included. Only sows that did not return to estrus after insemination in the first estrus after weaning were included in the analysis of litter size, piglet birth weight, piglet mortality, and subsequent sow BW, backfat depth, and loin muscle depth at the subsequent farrowing. If the interaction was not significant (P > 0.05), it was excluded from the models. Results are presented as least squares means ± SEM or as percentages (farrowing rate and piglet mortality). Differences at P < 0.05 were considered significant.

For the outcome variables farrowing rate and litter size, relations were tested with losses of sow BW, backfat, and loin muscle depth during lactation. In addition, relations of farrowing rate and litter size with body weight, backfat, and loin muscle depth gain during

the treatment period were tested. These variables were included in a model with parity and treatment together with all 2-way interactions. In a backward analysis procedure, the least significant interaction or variable was eliminated from the model until the model contained only significant variables. The outcome variable CVpbw was corrected for litter size because larger litters are related to a larger CVpbw (Quesnel et al., 2008).

3. RESULTS

Lactational variables preceding treatment were similar for the 3 treatments (results not shown) but were affected by parity (Table 5.2). First-parity sows had smaller litter sizes compared with second-parity sows (total born, P = 0.012; Table 5.2), whereas number of piglets weaned was not different. At weaning, piglets weaned from first-parity sows were 0.8 kg lighter compared with piglets weaned from second-parity sows (P < 0.0001; Table 5.2). Lactation length was 1.1 d shorter for first-parity sows compared with second-parity sows (P < 0.0001; Table 5.2). Sow body weight loss during lactation was not different between first- and second-parity sows, but first-parity sows were 26.9 kg lighter at weaning compared with second-parity sows (P < 0.001; Table 5.2). First-parity sows lost 1.8 mm more loin muscle during lactation compared with second-parity sows (P = 0.019, Table 5.2), whereas loin muscle at weaning was 2.5 mm smaller for first-compared with second-parity sows (P = 0.005; Table 5.2). Back fat loss during lactation and back fat at weaning were not different between parities (Table 5.2).

3.1 Gestation

Feed intake during the 30 day treatment period was 29% greater for the plus feed group (93.2 ± 0.4 kg) compared with the control and plus protein groups (72.3 ± 0.4 and 72.1 ± 0.4 kg, respectively, P < 0.0001).

3.2 Sow body weight, Backfat, and Loin Muscle

Table 5.3 shows body weight, backfat, and loin muscle at the start, during, and after treatment by treatment group and parity. No interaction between treatment and parity was found (P > 0.05). During treatment, sows in the Plus Feed group gained, respectively, 8.7 and 7.3 kg more body weight than sows in the Control and Plus Protein groups (P ≤ 0.001; Table 5.3). At the end of treatment, sows in the Plus Feed group were 10 kg heavier and had 1.5 mm more backfat than sows in the Control group. Sows in the Plus Protein group were intermediate (P = 0.02; Table 5.3). At farrowing, sows in the plus feed group still had 1.5 mm thicker backfat than Control sows, and sows in the plus protein group were intermediate (P ≤ 0.01; Table 5.3). Loin muscle depth before and during body weight gain and after treatment was not affected by treatment (Table 5.3).

Table 5.1 Composition of the experimental gestation diets (as fed basis)

Ingredient (%)	Standard gestation diet	Plus Protein gestation diet
Corn	17.70	16.12
Barley	15.80	14.00
Wheat	9.20	5.00
Wheat middlings	9.10	8.90
Wheat gluten feed meal	7.50	7.50
Palm oil, raffinated	0.50	0.50
Soybean oil	0.30	0.30
Molasses, cane	4.50	4.00
Sugar beet pulp < 10% sugar	8.50	8.00
Soybean hulls	7.00	5.10
Soybean meal, extracted		7.70
Linseed	0.90	0.90
Rapeseed, extracted	3.50	
Palm kernel meal	15.00	14.60
Whey concentrate	2.00	1.70
Phytase	0.03	0.04
Limestone	0.78	0.91
Vitamin E/Selenium	0.05	0.05
Salt	0.11	0.16
Sodium-Bicarbonate	0.38	0.14
Sow premix	0.50	0.50
Methionine		
Lysine 65%	0.37	0.25
Threonine 98%	0.06	0.02
Calculated content. %[1]		
Crude protein	11.78 ± 0.15	14.74 ± 0.14
Crude Fiber	9.51 ± 0.20	8.83 ± 0.20
Ash	5.64 ± 0.28	5.56 ± 0.28
Crude fat, extracted	4.29 ± 0.15	4.27 ± 0.14
Starch	26.42 ± 0.32	24.88 ± 0.31
Energy Value[2]	98.33 ± 0.16	99.20 ± 0.17
Ileal digestable lysine	0.47 ± 0.003	0.60 ± 0.003
Ileal digestable methionine	0.15 ± 0.002	0.19 ± 0.002
Ileal digestable methionine-cysteine	0.30 ± 0.004	0.36 ± 0.004
Ileal digestable threonine	0.29 ± 0.003	0.37 ± 0.003
Ileal digestable thryptophan	0.13 ± 0.177	0.13 ± 0.001

[1] Mean ± STD of the calculated values based on monthly analysis of the ingredients

[2] NE was calculated using the Dutch feedstuff table (CVB, 2007)

Table 5.2 Reproduction, sow body weight, back fat and loin muscle measures per parity before the treatment period (LSmean ± SEM)

Item	Parity	
	First	Second
	N = 100[1]	N = 45
Total number of piglets born (n)	12.7 ± 0.3[b]	14.0 ± 0.4[a]
Number of piglets weaned (n)	11.5 ± 0.1	11.6 ± 0.2
Average weaning weight piglets[2] (kg)	7.2 ± 0.1[b]	7.7 ± 0.1[a]
Lactation length (days)	26.2 ± 0.1[b]	27.3 ± 0.2[a]
Weaning to insmeination interval (d)	5.3 ± 0.1	5.3 ± 0.1
Weight loss during lactation (kg)	10.2 ± 0.6	10.5 ± 0.9
Weight loss during lactation (%)	20.0 ± 1.2	23.4 ± 1.8
Weight at weaning (kg)	173.8 ± 1.9[b]	200.7 ± 2.9[a]
Backfat loss during lactation (mm)	2.7 ± 0.3	3.4 ± 0.4
Backfat at weaning (mm)	14.9 ± 0.3	14.6 ± 0.4
Loin muscle depth loss lactation[2] (mm)	6.4 ± 0.6[a]	4.7 ± 0.7[b]
Loin muscle depth loss at weaning[2] (mm)	30.4 ± 0.5[b]	32.6 ± 0.7[a]

[a,b] LSmeans within a row without a common superscript differ (P < 0.05)

[1] One sow died shortly before farrowing and was therefore excluded from the analysis

[2] Corrected for the longer lactation length in second-parity vs. first-parity sows by adding lactation length as a covariable in the model,

At the start of treatment, second-parity sows were 26.1 kg heavier (P < 0.001; Table 5.3) and had 2.2 mm greater loin muscle depth (P = 0.01; Table 5.3) compared with first-parity sows. At the end of treatment, this difference in body weight was still 23.8 kg (P < 0.001; Table 5.3), whereas at farrowing, second-parity sows were only 13.7 kg heavier than first-parity sows (P = 0.001; Table 5.3). Body weight, backfat, and loin muscle gain per treatment were not different between parities.

3.3 Reproduction

Table 5.4 shows reproduction results per treatment group and parity. Effects of treatment on subsequent litter size and farrowing rate were similar for first- and second-parity sows. Sows in the Plus Feed group had a 13.2% smaller farrowing rate compared with those in the other treatments (P = 0.16; Table 5.4). Total number born from the first insemination, however, was greater for sows in the Plus Feed group (15.2 ± 0.5) compared with sows in the Control and Plus Protein groups (13.2 ± 0.4 and 13.6 ± 0.4 piglet, respectively, P = 0.006). As illustrated in Figure 5.1, sows in the Plus Feed group had fewer litters with ≤13 piglets and more litters with ≥17 piglets compared with sows in the other groups. Despite the larger litter size, average piglet birth weight was not different among treatments (P = 0.65; Table 5.4). Litters of sows in the Plus Feed group had a 3.8% larger within-litter birth weight variation compared with litters from Control sows (Table 5.4), and litters of sows in

Table 5.3 Sow body weight, backfat and loin muscle depth measures before, during and after the treatment period (main effects)[1]

Item	Treatment Group[2]			Parity		P-value	
	Control	Plus Feed	Plus Protein	1	2	Trt	Parity
Body weight at start treatment (kg)	183.6 ± 2.7	185.8 ± 2.8	189.0 ± 2.8	173.2 ± 1.9^b	199.3 ± 2.8^a	0.27	0.001
Body weight gain during treatment (kg)	15.5 ± 1.2^b	24.2 ± 1.2^a	16.9 ± 1.2^b	19.9 ± 0.8	17.8 ± 1.2	0.001	0.16
Body weight at end of treatment (kg)	199.8 ± 2.6^b	209.8 ± 2.7^a	205.9 ± 2.6^{ab}	193.3 ± 1.8^b	217.1 ± 2.7^a	0.02	≤ 0.001
Body weight after 2nd farrowing[3] (kg)	228.3 ± 3.3	233.5 ± 3.7	234.6 ± 3.4	225.3 ± 2.4^b	239.0 ± 3.4^a	0.36	0.001
Back fat at start treatment (mm)	13.9 ± 0.4	14.9 ± 0.4	14.3 ± 0.4	14.3 ± 0.2	14.4 ± 0.4	0.19	0.77
Back fat gain druing treatment (mm)	1.0 ± 0.3	1.5 ± 0.3	1.2 ± 0.3	1.2 ± 0.2	1.3 ± 0.3	0.56	0.87
Back fat at end of treatment (mm)	14.9 ± 0.4^b	16.4 ± 0.4^a	15.6 ± 0.4^{ab}	15.6 ± 0.2	15.7 ± 0.4	0.02	0.77
Back fat after 2nd farrowing[3] (mm)	16.5 ± 0.4^b	18.0 ± 0.4^a	17.7 ± 0.4^{ab}	17.9 ± 0.3	16.9 ± 0.4	0.01	0.06
Loin muscle depth at start treatment (mm)	33.5 ± 0.7	32.9 ± 0.7	33.2 ± 0.7	32.1 ± 0.5^b	34.3 ± 0.7^a	0.88	0.01
Loin muscle depth gain druing treatment (mm)	2.5 ± 0.6	3.6 ± 0.6	3.2 ± 0.6	3.6 ± 0.4	2.6 ± 0.6	0.37	0.14
Loin muscle depth at end of treatment (mm)	35.8 ± 0.7	36.6 ± 0.7	36.2 ± 0.7	35.7 ± 0.4	36.7 ± 0.7	0.64	0.25
Loin muscle depth after 2nd farrowing[3] (mm)	38.4 ± 0.7	36.9 ± 0.8	38.2 ± 0.7	38.4 ± 0.5	37.2 ± 0.7	0.33	0.18

^{a,b} Lsmeans within as row without a common superscript differ (P < 0,05)

[1] Interactions between treatment and parity were not significant. Therefore, LSmeans from models without interactions are presented

[2] All sows including repeat breeders; Control (2.5 kg/day; N = 49), Plus Feed (3.25 kg/day; N = 47), Plus Protein (2.5 kg/day added 30% digestible AA, N = 49),

Parity 1 (N = 100), Parity 2 (N = 45)

[3] Excluding repeat breeders; Control (N = 44), Plus Feed (N = 36), Plus Protein (N = 44), Parity 1 (N = 83), Parity 2 (N = 41)

the Plus Protein group were intermediate (P = 0.009; Table 5.4). However, after correction for litter size, the differences in litter CVpbw between sows in the Plus Feed and Control groups were not significant (19.7 ± 1.0% vs. 17.1 ± 0.9%, respectively, P = 0.13). Piglet mortality between d 1 and 3 was not different among treatments (P = 0.62; Table 5.4). Litter size was 2.4 piglet greater for second-parity sows compared with first-parity sows (P ≤ 0.001; Table 5.4). Average piglet birth weight was 110 g less for second-parity sows compared with first-parity sows (P = 0.006; Table 5.4). The CVpbw was 3.7% greater for second- parity sows compared with first-parity sows (Table 5.4). This difference decreased to 2.8% when corrected for litter size (20.1 ± 0.9% vs. 17.7 ± 0.6%, P = 0.05). Piglet mortality was not different between parities (P = 0.152; Table 5.4).

Table 5.4 Reproductive performance of sows after the treatment period per treatment group and parity (main effects)[1]

Item	Treatment Group[2]			Parity		P-value	
	Control	Plus Feed	Plus Protein	1	2	Trt	Parity
Farrowing Rate (%)	89.8	76.6	89.8	83.0	91.1	0.149	0.158
	(44/49)	(36/47)	(44/49)	(83/100)	(41/45)		
Total number of piglets born[3] (n)	13.2 ± 0.4[b]	15.2 ± 0.5[a]	13.6 ± 0.4[b]	12.7 ± 0.3[b]	15.1 ± 0.4[a]	0.006	0.001
Number of piglets born alive[3] (n)	12.6 ± 0.4[b]	14.4 ± 0.4[a]	13.2 ± 0.4[ab]	12.1 ± 0.3[b]	14.6 ± 0.4[a]	0.008	0.001
Average birth weight piglets[3] (kg)	1.45 ± 0.03	1.42 ± 0.04	1.46 ± 0.04	1.50 ± 0.02[a]	1.39 ± 0.03[b]	0.650	0.006
CV birth weight[3] (%)	16.9 ± 0.9	20.7 ± 1.0[a]	19.9 ± 0.9[ab]	17.3 ± 0.6[b]	21.0 ± 0.9[a]	0.009	0.001
Piglet mortality from day 1 to 3 (%)	8.7%	10.3%	8.4%	7.4%	11.3%	0.625	0.152

[a,b] LSmeans within as row without a common superscript differ (P < 0,05)

[1] Interactions between treatment and parity were not significant. Therefore, LSmeans from models without interactions are presented

[2] Control (2.5 kg/day; N = 49), Plus Fed (3.25 kg/day; N = 47), Plus Protein (2.5 kg/day added 30% digestible AA, N = 49)

[3] From 1st insemination (e.g without repeat breeders)

3.4 Lactation Losses and Gestational Gain in Relation to Treatment
Litter size after treatment was not significantly affected by back fat losses during lactation or by body weight, back fat, or loin muscle depth gain during treatment. Body weight losses and loin muscle depth loss during lactation, however, significantly affected litter size after treatment. For every kilogram of body weight loss during lactation, subsequent litter size decreased by 0.04 piglet (P = 0.02) and for every millimeter of loin muscle depth loss, subsequent litter size decreased by 1.8 piglets (P = 0.006). Farrowing rate after treatment was not significantly affected by body weight, back fat, or loin muscle depth losses during lactation or by their gain during treatment.

4.0 DISCUSSION

This study showed that a 30% greater feed intake from days 3 to 32 after insemination in first- and second parity sows (during the second and third gestation, respectively) increased body weight gain during early pregnancy and increased litter size without affecting average birth weight. However, the increased feeding level also gave a numerically reduced farrowing rate. Feed with 30% extra protein did not improve body weight gain or reproductive performance.

The finding that the plus feed treatment resulted in a larger litter size indicates increased embryonic and fetal survival. This is illustrated by the relatively large percentage of litters with ≥17 piglets in the Plus Feed group (28%) compared with the Control group (7%). Despite the average of 2 more piglets per litter, piglet birth weight was not decreased in the plus feed treatment, which indicates improved embryonic and fetal development. An increased feeding level might alter metabolic or endocrine pathways, or both, which could positively influence embryonic and fetal survival and development. An increased feeding level during early pregnancy increased GH and IGF-1 concentrations in plasma, as well as uterine flushings, which could directly or indirectly influence embryonic development and survival (De et al., 2009). For example, Block et al. (2003) reported that in vitro-produced bovine embryos that were cultured in IGF-1-enriched media showed a greater percentage of blastocysts on days 7 and 8 after fertilization, and a greater embryo survival after transfer compared with embryos cultured in media without IGF-1. Furthermore, IGF-1 also influenced progesterone production during the early luteal phase. For example, Langendijk et al. (Langendijk et al., 2008) reported a positive correlation (r = 0.7) between IGF-1 concentration around day 1 after ovulation and the increase in progesterone concentration during early gestation in primiparous sows.

Between days 12 and 29 of gestation, progesterone production is dependent on LH secretion (Peltoniemi et al., 1995; Tast et al., 2000; Khan et al., 2007). Luteinizing hormone secretion, in turn, is positively influenced by feeding level, especially in periods of seasonal infertility (Peltoniemi et al., 1997; Virolainen et al., 2004). An increased feeding level can therefore stimulate embryonic development, thereby increasing survival by increasing progesterone production through increased LH secretion after day 12 of gestation. Fetal development is expected to be compromised when litter size increases, which is related to compromised placental development in crowded uteri (Vonnahme et al., 2002; Town et al., 2005; van der Waaij et al., 2010). An increased feeding level during the first 4 wk of gestation might also improve embryonic and placental development through an increased availability of specific micronutrients, such as folic acid and arginine (Matte et al., 1996; Hazeleger et al., 2007). Supplementation of arginine improved placental vascularization (Hazeleger et al., 2007), which may be the critical factor determining placental efficiency. A high placental efficiency can, in turn, increase litter size and piglet birth weight, as was shown by Ramaekers et al.(2006). Even though the feed in the current experiment was not supplemented, feeding more feed, and therefore giving more nutrients, might have had similar effects as supplementation of specific nutrients and AA. Thus, an increased feeding level might stimulate embryonic and placental development, and thereby embryo survival, by its influence on IGF-1. Insulin-like growth factor 1 stimulates embryo development and progesterone production during the early luteal phase by its stimulating effect on LH, and therefore progesterone production after day 12 of pregnancy. Increased feeding may also increase embryo survival by increasing the availability of micronutrients such as arginine. In addition to the positive effects on litter size, the increased feeding level numerically

reduced farrowing rate. For gilts, it is known that an increased feeding level from days 1 to 15 after insemination can have a negative effect on embryonic survival (Ashworth, 1991; Pharazyn, 1992; Jindal et al., 1996). A recent study by Quesnel et al. (2010), however, showed that an increased feeding level from days 1 to 7 after insemination did not affect embryonic survival in gilts. For multiparous sows, no negative effects of an increased feeding level during early pregnancy have been reported (e.g., Varley and Prime (1993), days 1 to 25; (e.g., Varley and Prime (1993), days 1 to 25; Virolainen et al. (2005b)).

Figure 5.1. Percentage of sows, per treatment, with a litter size of ≤ 10, 11 to 13, 14 to 16 or ≥ 17 piglets after treatment (Control (2.5 kg/d), Plus Feed (3.25 kg/d), Plus Protein (2.5 kg /d with 30% added ileal digestible AA)).

Negative effects of an increased feeding level on embryonic survival in gilts have been related to reduced plasma progesterone concentrations in animals on an increased feeding level (Ashworth, 1991; Jindal et al., 1996; van den Brand et al., 2000b; Virolainen et al., 2005a) because of increased progesterone clearance in the liver (Prime and Symonds, 1993). A sufficiently increased progesterone concentration is necessary for synchronous uterine and embryonic development during early pregnancy (Pope, 1988; Ashworth, 1992). If an increased feeding level results in reduced progesterone concentrations during the first 2 weeks of gestation, pre-attachment embryonic survival might be affected, possibly even causing a failure of maternal recognition of pregnancy in some sows with small numbers of embryos. This might explain why sows on the increased feeding level had fewer litters with ≤13 piglets compared with the Control group (≈30 vs. ≈54%, respectively). On the other hand, Sørensen and Thorup (2003) also studied the effects of increased feeding
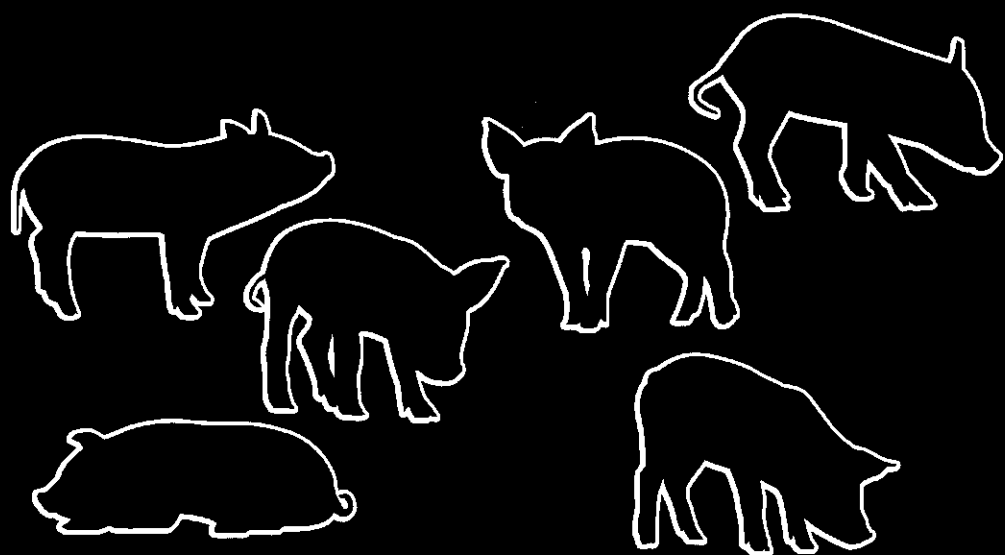
levels during the first 28 d of pregnancy in sows and found positive effects on litter size (+0.5 piglet), but no negative effects on farrowing rate (86.4 vs. 86.9%). In our study, the 13% difference in farrowing rate was not statistically significant. To prove such a difference, the number of animals per treatment groups should have been increased to 90 (Win Episcope, Edinburgh, UK; Thrusfield et al., 2001). However, our main interest in the present study was to examine litter size effects of the feeding regimen. Therefore, the number of animals per treatment was set at 50, which is sufficient to statistically prove a difference of 1.5 piglets with a SD of 3, 95% confidence, and a power of 80% (Win Episcope). If the 13% smaller farrowing rate had been significantly different, the economic gain attributable to a larger litter size in the plus feed group would have outweighed the costs by the increase in non-productive days in the plus feed group. For example, based on a gestation length of 115 d, a lactation length of 25.3 days, and a weaning-to- insemination interval of 5.6 days, and 30 non-productive days for repeat breeders (Agrovision BV, Deventer, the Netherlands), the maximum farrowing index that could be achieved for non-repeat breeders and repeat breeders would be 2.5 and 2.1 litters per year, respectively. The Control group showed 90% non-repeat breeders (litter size of 12.6 piglets) and 10% repeat breeders (litter size of 15.2 piglets, results not shown). The plus feed group showed 77% non-repeat breeders (litter size of 14.4 piglets) and 23% repeat breeders (litter size of 16.2 piglets, results not shown). For a 100-sow farm with sows in only the Control or plus feed group, the average piglet production per year would be 31.5 and 35.2 piglets, respectively. The extra piglets in the plus feed group would therefore compensate for the increase in non-productive days. In contrast to the plus feed treatment, the plus protein treatment did not significantly improve sow recovery or reproduction. Clowes et al. (2003a, b) reported that protein losses during lactation have a large influence on subsequent reproduction. It was therefore hypothesized that feeding extra protein during early gestation could improve recovery as well as reproduction. However, energy is needed for the utilization of feed protein for body protein (Campbell et al., 1985). If extra protein is supplied but the energy supply is not sufficient, the expected gain in body protein may not be seen. Indeed, in our study, BW gain and loin muscle gain were not significantly improved in sows in the plus protein group compared with Control sows. Sows in the plus feed group received both extra protein and extra energy, and could therefore benefit from the extra protein, as is shown by the extra BW gain in the plus feed group. Thus, extra protein does not affect sow recovery when not accompanied by extra energy, nor does it have an effect on reproductive output. Early gestation may be the best period for a sow to recover from lactational losses (Dourmad et al., 1996). During this period, the energy demand for fetal growth is still decreased, and energy and nitrogen from the feed can be used for maternal tissue accretion (Dourmad et al., 1996).

In the present study, the increased feeding level increased BW gain during early pregnancy, indicating a greater compensation of the lactational BW losses compared with the standard feeding level. In addition, no relations between loss of body reserves during lactation and

recovery of body reserves during early gestation with reproduction in subsequent parity were found, but the number of sows per treatment might be too small for such an analysis. The finding that the increased feeding level had similar effects in both first- and second-parity sows shows that this strategy is beneficial for both parities. In conclusion, this study showed that an increased feeding level during the first 4 wk of the second (for first-parity sows) and third (for second-parity sows) gestation improved sow BW gain and increased litter size by 2 piglets. Farrowing rate, however, may be negatively affected.

Acknowledgements

Chapter 6

Embryonic survival, progesterone profiles and metabolic responses to an increased feeding level during second gestation in sows.

Embryo survival, progesterone profiles and metabolic responses to an increased feeding level during second gestation in sows

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ABSTRACT

This study describes reproductive and metabolic responses in sows fed at two different feeding levels from days 3–35 of second gestation. After insemination, 37 sows were assigned to one of two treatments: 1) Control: 2.5 kg/day of a gestation diet; 2) Plus Feed: 3.25 kg/day of a gestation diet (+30%). Sow weight, back fat and loin muscle depth were measured at farrowing, weaning, start of treatment, day 14 after start treatment and end of treatment. Frequent blood samples were taken for progesterone, luteinizing hormone (LH), glucose and insulin, insulin-like-growth-factor-1 (IGF-1), non-esterified-fatty-acids (NEFA) and urea analysis. At day 35 after insemination sows were euthanized and their reproductive tract collected to assess ovarian, embryonic and placental characteristics. Plus Feed sows gained 5.4 kg more weight and 0.9 mm more back fat and tended to be heavier at slaughter compared to Control sows (193 vs. 182 kg, P ± 0.06). No difference in loin muscle gain was found. Treatment also did not affect vital embryonic survival, which was 72.1 ± 3.9% for Control and 73.4 ± 3.2% for Plus Feed sows, resulting in, respectively, and 15.9 ± 0.9 and 15.7 ± 0.7 vital embryos. No effect of treatment on any of the ovarian, embryonic or placental characteristics was found. Progesterone profiles during the first month of gestation, and LH characteristics at day 14 of gestation were not different between treatments. Progesterone concentration was lower (P < 0.05) 3 h after feeding compared with the pre-feeding level on days 7–11 after first progesterone rise for Plus Feed and on days 8–10 after first progesterone rise for Control sows. At day 15, pre-prandial glucose and insulin concentrations were not different between treatments, insulin peaked later (48 vs. 24 min) and at a higher concentration in Plus Feed than in Control sows. Furthermore, glucose area under the curve (AUC) tended to be lower (-171.7 ± 448.8 vs. 1257.1 ± 578.9 mg/6.2 h, P = 0.06, respectively) for Plus Feed vs. Control sows. IGF-1 concentration was not different between treatments, but NEFA concentrations were lower for Plus Feed vs. Control sows (149.5 ± 9.2 vs. 182.4 ± 11.9 m/L, respectively, P = 0.04) and urea concentration tended to be higher in Plus Feed than in Control sows (4.3 ± 0.1 vs. 3.9 ± 0.1, respectively, P = 0.13). None of the metabolic parameters were related to reproductive measures. In conclusion, feeding 30% more feed from day 3 till day 35 of second gestation increased weight gain and resulted in lower NEFA concentrations, but did not affect progesterone, LH or IGF-1 and embryonic and placental characteristics.

Keywords: Sow, Reproduction, Feeding Level, Metabolism, Progesterone

1. INTRODUCTION

Lactation weight losses in sows can be substantial, especially in primiparous sows in which weight losses can reach up to 20 to 30 kg (Clowes et al., 2003b; Eissen et al., 2003; Hoving et al., 2010; Schenkel et al., 2010). These losses have been related with reduced subsequent reproductive performance (Clowes et al., 2003b; Thaker and Bilkei, 2005). An increased feed intake during the early stages of the subsequent pregnancy may help to quickly recover from these lactation losses and thereby overcome the negative effects on farrowing rate and litter size in subsequent parity. In gilts, however, several studies have found a negative effect of an increased feed intake during early pregnancy on embryonic survival (Pharazyn, 1992; Jindal et al., 1996; De et al., 2009), although a recent study did not substantiate this (Quesnel et al., 2010). In multiparous sows, embryonic survival does not seem negatively affected by feeding level in early pregnancy (Heap et al., 1967; Toplis and Ginesi, 1983; Varley and Prime, 1993; Virolainen et al., 2005b). In contrast, Sørensen and Thorup (2003) reported significant positive effects on litter size, +0.3 piglets, when sows were fed 49.9 vs. 31.2 MJ ME day^{-1} in the first 28 days after insemination. Also a recent study by Hoving et al. (2011) found positive effects of an increased feed intake in the first month of pregnancy of first and second parity sows (39.0 vs. 30.0 MJ ME day^{-1}) on subsequent litter size (-2 piglets). Thus, whereas most gilt studies find that a high feeding level in early pregnancy lowers embryonic survival, older parity sows may have equal or higher embryo survival at a high feeding level. Lower embryonic survival in gilts on a high feeding level has been related to decreased systemic progesterone concentrations (Pharazyn, 1992; Jindal et al., 1996), caused by an increased clearance in the liver related with an increased metabolic rate (Prime and Symonds, 1993). Injections of exogenous progesterone in gilts on a high feeding level, to restore progesterone concentrations in high fed gilts, have shown to alleviate the negative effects of feeding level on embryonic survival (Ashworth, 1991; Jindal et al., 1997). Besides the negative effects of metabolic clearance on progesterone concentrations, a higher feed intake may also have a positive effect on progesterone concentrations. Insulin like growth factor-1 (IGF-1) and insulin are both positively influenced by feeding level (De et al., 2008) and Langendijk, et al. (2008) reported a positive correlation ($r = 0.7$) between IGF-1 concentration on day 1 after ovulation and early progesterone rise (12–36 h after ovulation). Furthermore, Yuan and Lucy (1996) reported an increase of in vitro progesterone production in large luteal cells when these cells were incubated with 100 ng/mL IGF-1. Besides this direct effect, insulin or IGF-1 may also have an indirect effect on progesterone production via stimulation of luteinizing hormone (LH) secretion by the pituitary (Barb et al., 2001). Furthermore, endometrial IGF-1, its receptors and binding proteins play an important direct role in early embryonic development and placentation (reviewed by Geisert and Yelich (1997)), and might be influenced by systemic IGF-1 concentrations (Simmen et al., 1998). Between day 12 and day 29 of gestation, progesterone production is largely dependent on LH stimulation (Peltoniemi et al., 1995; Tast et al., 2000; Khan et al., 2007). Higher feeding

levels have been found to increase LH secretion (Peltoniemi et al., 1997), which might subsequently increase progesterone production after day 12 of pregnancy. So, feeding level can affect embryonic development and survival by different pathways, several of them involving progesterone dynamics. In second parity sows, i.e., sows weaned from their first litter, progesterone concentrations and relationships with embryo survival, related to feeding level, may be markedly different from gilts, since these sows have suffered substantial weight losses and need to restore their body reserves. Metabolic indicators for fat and nitrogen metabolism (respectively, non-esterified-fatty-acids (NEFA) and urea) are therefore also measured in this study. Hoving, et al. (2011) showed that feeding sows 30% more feed during early second or third gestation, improved sow body development as well as reproductive performance. This study aims to find physiological explanations for these effects of feeding level on litter size, by describing reproductive and metabolic responses in sows fed different feeding levels during the day 3–35 of second gestation.

2. MATERIALS AND METHODS

All experimental procedures were approved by the Institutional Animal Use and Care Committee of Wageningen University (Wageningen, the Netherlands).

2.1. Animals, housing and feeding

In total, 37 crossbred (Yorkshire x Dutch Landrace) first parity sows were used. Between October and December 2010, the animals arrived in three batches (n = 10, n = 14 and n = 13, respectively) at day 80 ± 4 of first pregnancy at the experimental farm 'de Haar' of Wageningen University in Wageningen, the Netherlands. On day 103 ± 0.5 of first gestation, sows were fitted with an indwelling jugular vein catheter as described by Soede, et al. (1997), to allow frequent blood sampling. After surgery, sows were housed in individual farrowing crates. From day 2 after surgery, gestation feed was gradually, in a 7-day period, replaced with the commercial lactation diet (13.1 MJ ME/kg, 15.5% Crude protein and 0.8% lysine) which was fed throughout lactation. Within 3 days after farrowing, litters were standardized to 11 to 13 piglets. Feed allowance gradually increased in the first 14 days of lactation to a maximum of 7 kg, which was based on sow body weight after farrowing and number of piglets suckling (1% of body weight for maintenance and 0.4 kg per piglet). After weaning (day 25.5 ± 1.4), sows were housed in individual gestation crates. From weaning to insemination, sows were fed 3.5 kg/day of the lactation diet. Sows were checked for estrus two times per d (0900 and 1530 h) using the back pressure test in the presence of a mature teaser boar. Four to 6 h after first standing estrus, sows were inseminated with a commercial dose of semen (1.5 x 10^9 motile sperm cells of a TOPIGS boar line, Topigs, Vught, the Netherlands). If still in estrus, sows received a second or third insemination 21 to 24 h after first or second insemination. Throughout the experiment the animals were fed twice a day (0830 and 1600 h) and had ad libitum access to water.

2.2. Gestation and treatments

Sows remained individually housed in gestation crates. From insemination to start of the treatment sows were fed 2.5 kg/day of the gestation diet (Table 6.1). After insemination, sows were divided into one of two treatments based on percentage weight loss during lactation (on average 14.5 ± 6.0%, 29.3 ± 12.7 kg) and weaning to insemination interval (on average 4.8 ± 0.7 days). The treatments were 1) Control: 2.5 kg/day of the gestation diet (Table 6.1), 2) Plus Feed: 3.25 kg/day of the gestation diet. Treatments were applied from day 3 after first insemination until slaughter at day 35.4 ± 0.6 after first insemination.

Table 6.1 Composition of the gestation diet (as fed basis)

Ingredient (%)	
Corn GMO	12.5
Barley	24.95
Wheat Boat	5
Wheat Grits	15
Wheat gluten feed meal	10
Soybean oil	0.32
Molasses, beet	2.5
Sugarbeetpulp, <10% sugar	8.09
Linseed	1.5
Rapeseed, extracted	2.25
Sunflowerseed, extracted	3.5
Palm kernel meal	10
Whey concentrate	1
Monocalcium-phosphorus	0.48
Lime	1.09
Vitamin E/Selenium	0.09
Salt	0.15
Sodium-bicarbonate	0.31
Sow premix	0.50
Lysine 65%	0.29
Threonin 98%	0.03
Calculated content (%)	
Crude Protein	13
Crude Fiber	8.16
Ash	6.12
Crude Fat, extracted	3.76
Starch	30.55
Energy Value[a]	100

[a] NE was calculated according to the Dutch feedstuff table (CVB, 2007)

2.3. Measurements

During the treatment period feed refusals were collected daily and feed intake per sow was calculated weekly. From day 18 after first insemination onwards sows were checked for signs of estrus twice a day using fence line contact with a mature teaser boar. Around 4 wk of gestation an ultrasound check (Scanner 200, Pie Medical/Esaote, Maastricht, the Netherlands) was performed to confirm pregnancy.

2.3.1. Sow development

Sow body weight, backfat and loin muscle depth were measured one day after farrowing, at weaning, at start of treatment, 14 days after start of treatment and the day before slaughter. Back fat was measured 6 cm of the midline, straight above the last rib on the left and right side of the animal using a Renco© Meter (MS Schippers, Bladel, the Netherlands). Loin muscle depth was measured at the same locations using Aloka ultrasound Equipment (Aloka SSD-500, Biomedic Nederland BV, Almere, the Netherlands). For loin muscle measurement, two measurements were taken on both the left and right sides of the animal. If the two measurements at one side differed more than 2 mm a third measurement was taken. Because of technical problems, loin muscle depth after farrowing and at weaning was not measured in sows from Batch 1. Weight, back fat and loin muscle gain was calculated per sow as the difference between two time points (e.g., weight gain treatment period - weight at slaughter – weight at start of treatment, etc.).

2.3.2. Blood sampling

From day 4 after weaning, a 7 mL blood sample was taken twice a week (at 3–4-day interval) at 7:30 AM, for analysis of IGF-1, NEFA and urea. For these twice weekly samples, day 5 after weaning was defined to be day 0, which was at D - 0.1 ± 0.8 (mean ± SD) after first insemination.

From the day of first insemination (day 0) to day 20 of gestation, 3 mL blood samples were taken daily at 7:30 AM. After day 20, blood samples were taken three times per wk, with 2 to 3-day interval. In addition, from days 0–11 of gestation a 3 mL blood sample was taken 3 h after the morning meal (1130 h). All samples were analyzed for progesterone. On day 14.3 ± 0.6 after first insemination, blood samples were collected every 15 min from 0800 to 1800 h in 24 sows and analyzed for LH concentrations. On day 15.3 ± 0.6 after first insemination, a glucose and insulin profile was determined in all sows. Samples were taken at -24, -12, 0, 12, 24, 36, 48, 60, 84, 120, 156, 228, 300 and 372 min relative to the morning feeding at 8:30 AM. All sows finished their portion within 10 min after feeding. All blood samples (except for NEFA samples) were collected in polypropylene tubes containing 50 or 100 µL (depending on sample size) EDTA solution (144 mg/mL saline), were placed on ice and centrifuged at 3000g for 10 min at 4 °C. Plasma was collected and stored at -20 °C until analysis. NEFA samples were collected in 0.8-mL serum tubes (Minicollect, Greiner Bio-One BV, Alphen a/d Rijn, Netherlands). After collection the NEFA samples were

allowed to incubate at room temperature for at least 1 h, after which the samples were centrifuged at 3000g for 10 min. Serum was collected and stored at -20 °C until analysis.

2.3.4. Plasma analyses

Plasma progesterone concentrations were analyzed in duplicate using a commercial Coat-A-Count progesterone RIA-kit (PITKPG-7, Siemens Medical Solutions Diagnostics, Los Angeles, CA, USA). The sensitivity, intra- and interassay CV were 0.1 ng/mL, 4.7 and 6.0%, respectively. The average progesterone concentration was calculated as the mean of all values from days -1 to 34 (PD 1 = day of first progesterone rise above 0.5 mg/mL). Furthermore, average progesterone concentrations from PD 1 to 10, 11 to 15, 16 to 21 and 21 to 34 were calculated using all values in the defined time frame. Plasma LH concentrations were analyzed in duplicate, using homologous double antibody RIA, following the method described by Cosgrove, et al. (1991), with the following modifications: 1% BSA was used in the assay buffer, for the precipitation 50 µL cold Saccel (anti sheep/goat, IDS-AA-SAC2, Lucron Bioproducts BV, Gennep, the Netherlands) was used. After mixing and incubation for 1 h tubes were centrifuged at 6240g for 6 min at 4 °C, aspirated and counted. Porcine LH was supplied by the National Hormone and Peptide Program (NHPP, NIDDK, Dr Parlow, Harbor-UCLA Medical Center, Torrance, CA, USA). The sensitivity, intra- and interassay CV were 0.012 ng/mL, 7.0% (n = 73) and 6.5% (n = 15), respectively. Definition of LH pulses was done as described by Van Leeuwen, et al. (2011a). Basal LH concentration was calculated as the average of the six lowest values. Average LH concentration was calculated as the average of all values, including the peaks. The pulse amplitude was the difference between the maximum pulse value minus the previous nadir. The pulse area was defined as the sum of the maximum value and the four subsequent values minus the previous nadir. For glucose analyses, 500 µL 0.3 M trichloroacetic acid (TCA) was added to 50 µL of plasma for precipitation of protein. After centrifugation at 16 000g for 1 min, glucose concentrations in the supernatant were analyzed in duplicate with an enzymatic colorimetric assay using the glucose-oxidase-peroxidase (GODPAP) method using a commercial kit (Roche Diagnostics, Nederland BV, Almere, the Netherlands. Plasma insulin concentrations were analyzed in duplicate using a commerial RIA-kit (PI-12K Porcine insulin RIA-kit, Millipore, St Charles, MO, USA). The sensitivity was 2 µU/mL, and intra and interassay CV were 6.4% (n = 42) and 6.05 (n = 9), respectively. For both glucose and insulin, basal levels were calculated as the mean value of the two samples before feeding (t = -12 and 0), the area under the curve (AUC) was calculated as the area above the basal level from feeding until 372 min after feeding. The IGF-1 concentrations were quantified in duplicate, using a commercial kit (IRMA IGF-1 A15729, Immunotech, Marseille, France), after extraction of the samples with ethanol/HCl (as validated by Louveau and Bonneau (1996). The sensitivity, intra- and interassay CV were 2 ng/mL, 2.2% (n = 26) and 3.5% (n = 12), respectively. The NEFA concentrations were determined in duplicate using an enzymatic colorimetric assay using the Wako NEFA-HR (2) ACS-ACOD method (Wake chemicals, Neuss, Germany). Hundred µL of acetyl- CoA synthetase was added to 5-µL serum and then incubated for 10 min at

37 °C. After incubation, 50 µl of Acy-CoA oxidase was added to the serum mixture and it was incubated again for 10 min at 37 °C. After second incubation the extinction was measured with a spectrophotometer at a wavelength of 550 nm, using a standard curve formula the NEFA concentration was calculated. The sensitivity of the test was 0.1 mmol/L. Urea concentrations were also determined in duplicate using an enzymatic colorimetric assay (Urea liquicolor, Human, Wiesbaden, Germany), with a sensitivity of 66.6 mmol/L.

2.3.5. Reproductive measurements

Weaning to estrus interval, date and time of inseminations and date of return to estrus or confirmed non-pregnancy were recorded. At 35.4 ± 0.6 days after insemination, sows were slaughtered by stunning and exsanguination and their reproductive tracts were collected. The ovaries were removed and the number of CL counted. Luteal weight was determined after dissection of the CL from the ovaries. After removal of the mesometrium and separation of the uterine horns, the horns were cut open and the number of embryos were counted and classified as viable, based on size and color, or non-viable, based on strongly hemolyzed amniotic fluid, reabsorbed embryonic membranes, or both. After separating embryos and placentas, length and weight of embryos was determined. Placental length was measured immediately, while weight was determined after freeze drying for 72 h. Empty horns were weighed and measured and length of implantation sites was determined.

2.4. Statistical analysis

Of the 37 inseminated animals, two animals were not used in the analysis; one sow had only 7 CL and consistently low progesterone concentrations, already before treatment. Another sow became ill (fever) around day 20 after insemination, which resulted in termination of pregnancy around the same time. These sows were therefore excluded from the calculation of pregnancy rate. Only sows that remained pregnant until d 35 after insemination (32 out of 35 sows) were used in the subsequent analyses. Data were analyzed using SAS (SAS Inst., Inc., Cary, NC, USA) and are presented as LSmean ± SEM, unless stated otherwise. Embryonic survival was calculated as the percentage of CL represented by a (vital) fetus (Jindal et al., 1997). For all parameters, normality was checked using the UNIVARIATE procedure. Sow weight, back fat and loin muscle depth development were analyzed using the Mixed procedure in SAS, with Treatment (Control, Plus Feed), Batch (1, 2, 3) and time (weaning, start treatment, d 14 after start treatment, d before slaughter) as fixed effect. Sow was added as a repeated measures effect. All profile analysis were done using the Mixed procedure in SAS, with sow added as a repeated measures effect and with the interaction term treatment * day or treatment * time added to the model. Progesterone profiles were analyzed with Treatment (Control, Plus Feed), Batch (1, 2, 3) and day (-1 to 35) as fixed effect. For analysis of the effect of sampling time within d, Time (0730 or 1130 h) was added to the above model as a fixed effect. Glucose and insulin profiles were analyzed with Treatment (Control, Plus Feed), Batch (1, 2, 3) and Time (-24, -12, 0. . . . , Three hundred,

372) as fixed effect. Metabolic profiles (IGF-1, Urea and NEFA) were tested with Treatment (Control, Plus Feed), Batch (1, 2, 3), and day (-1, 3, 6, 10, 13, 17, 20 and 35) as fixed effect. In addition, average value of the seven gestation metabolic samples (day 3, 6, 10, 13, 17, 20, 35) was calculated.

Embryonic and placental characteristics, average progesterone and LH characteristics, basal glucose and insulin concentration and area under the curve, average IGF-1, NEFA and urea concentrations, weight, back fat and loin muscle gain were analyzed using the GLM procedure in SAS, with treatment (Control, Plus Feed), batch (1,2,3) and their interaction as fixed effects. Preliminary analysis showed that the interaction was never significant and it was therefore excluded from the model. For embryo weight and length and placental weight and length, age at slaughter was added to the above model as a covariate. Pearson's correlation coefficients were used to determine relationships between continuous variables. Preliminary analysis showed strong correlations between the average progesterone value from d 11 to 15 and the progesterone values from d 1 to 10 ($r = 0.92$), 16 to 20 ($r = 0.61$) and 21 to 35 ($r = 0.48$). Considering the fact that LH, glucose and insulin were measured on d 14 and 15 of gestation, we only present correlations from the d 11 to 15 values. To test if correlations were different between treatments, one variable was added to a linear model containing treatment (Control, Plus Feed) and Batch (1, 2, 3) and the interaction treatment * variable. The other variable was used as a dependent variable. If the treatment * variable interaction was significant, correlation coefficients are presented per treatment.

3. RESULTS

Daily feed intake during the treatment period was 28% higher for the Plus Feed compared with the Control sows (104.1 ± 1.2 vs. 81.4 ± 1.4 kg, respectively, $P = 0.0001$). Data on sow weight, back fat and loin muscle depth development are shown in Table 6.2. On average, sows in the Plus Feed group gained 5.4 kg more weight during the treatment period compared with sows in the Control group (20.3 ± 1.3 vs. 14.9 ± 1.6 kg, respectively, $P = 0.01$), which was largely due to higher weight gain in the 14 days after start of treatment for the Plus Feed group compared with the Control group (7.3 ± 0.7 vs. 3.3 ± 0.9 kg, respectively, $P = 0.02$). As a result, Plus Feed sows tended to be heavier at day 14 (180.6 ± 2.9 vs. 170.0 ± 3.5, respectively, $P = 0.08$) and at slaughter (193.4 ± 2.9 vs. 182.0 ± 3.5, respectively, $P = 0.06$) than Control sows. Back fat and loin muscle depth were not significantly different between treatments at any time. Plus Feed sows, however, gained 0.9 mm more back fat during the treatment period compared with the Control sows (0.8 ± 0.2 vs. 1.7 ± 0.2 mm, respectively, $P = 0.006$).

Table 6.2 Weight, back fat and loin muscle depth measures per treatment for pregnant sows (LSmeans ± SEM)

	Control	Plus Feed	P value treatment
Number of sows (n)	13	19	
Weight at weaning (kg)	169.4 ± 3.5	172.3 ± 2.9	0.53
Weight at start of treatment (kg)	166.8 ± 3.5	173.2 ± 2.9	0.17
Weight at day 14 after start of treatment (kg)	170.0 ± 3.5	180.6 ± 2.9	0.08
Weight before slaughter (kg)	182.0 ± 3.5	193.4 ± 2.9	0.06
Back fat at weaning (mm)	13.1 ± 0.7	12.2 ± 0.6	0.31
Back fat at start of treatment (mm)	12.6 ± 0.7	12.6 ± 0.6	0.91
Back fat at day 14 after start of treatment (mm)	13.5 ± 0.7	13.5 ± 0.6	0.99
Back fat before slaughter (mm)	13.4 ± 0.7	14.3 ± 0.6	0.32
Loin muscle depth at weaning (mm)	35.2 ± 1.1	34.9 ± 0.9	0.84
Loin muscle depth at start of treatment (mm)	36.1 ± 1.0	37.6 ± 0.8	0.36
Loin muscle depth at day 14 after start of treatment (mm)	37.7 ± 1.0	39.1 ± 0.8	0.40
Loin muscle depth before slaughter (mm)	39.0 ± 1.0	41.0 ± 0.8	0.12

3.1. Pregnancy, embryonic and placental development

Pregnancy rate was 87% (13/15) for the Control group and 95% (19/20) for the Plus Feed group (P = 0.40). Ovulation rate was 22.6 ± 1.0 for Control and 21.5 ± 0.9 for Plus Feed sows, which resulted in, respectively, 15.9 ± 0.9 and 15.7 ± 0.7 viable embryos, representing an embryonic survival rate of, respectively, 72.1 ± 3.9 and 73.4 ± 3.2%. Embryonic and placental characteristics, however, were not significantly different between treatments (Table 6.3).

3.2. Progesterone profiles

No significant differences in progesterone profiles were found between treatments (Figure 6.1). For both treatments, progesterone concentration rapidly increased until day 12 (average 33.9 ± 1.1 ng/mL), after which it gradually decreased until day 22 and stabilized thereafter (average 21.5 ± 1.1 ng/mL, Figure 6.1). Progesterone concentrations were significantly lower in the postprandial samples compared with the preprandial samples on days 8–10 in the Control group and on days 7–11 in the Plus Feed group (P < 0.05, Fig. 6.2).

3.3. LH

The LH characteristics at day 14 of pregnancy were not different between treatments (Table 6.4). A negative correlation (r = -0.45, P = 0.04, n = 21) was found between basal LH concentration on day 14 of pregnancy and average progesterone concentration from days 11 to 15.

Table 6.3 Embryonic and placenta characteristics per treatment (LSmeans ± SEM)

	Control	Plus Feed	P value treatment
Number of sows (n)	13	18[a]	
Ovary			
Number of CL (n)	22.6± 1.0	21.5 ± 0.9	0.42
Luteal Weight (g)	8.1 ± 0.3	8.1 ± 0.3	0.87
Number of Embryos			
Total (n)	17.9 ± 1.1	17.7 ± 0.9	0.88
Vital (n)	15.9 ± 0.9	15.7 ± 0.7	0.84
Embryonic Survival			
Total (%)	79.2 ± 4.2	82.3 ± 3.5	0.69
Vital (%)	72.1 ± 3.9	73.4 ± 3.2	0.80
Viable embryos/implantation Sites (%)	86.4 ± 2.4	87.6 ± 2.0	0.69
Embryonic Development[b]			
Length (cm)	3.8 ± 0.07	3.8 ± 0.06	0.78
Within sow std (cm)	0.18 ± 0.03	0.18 ± 0.02	0.84
Weight (g)	4.1 ± 0.2	4.2 ± 0.1	0.72
Within sow std (g)	0.4 ± 0.1	0.4 ± 0.1	0.94
Placental Development[b]			
Length (cm)	35.4 ± 1.6	37.3 ± 1.4	0.39
Within sow std (cm)	8.6 ± 0.7	9.5 ± 0.6	0.37
Weight (g)	1.9 ± 0.1	2.0 ± 0.1	0.72
Within sow std (g)	0.49 ± 0.04	0.48 ± 0.04	0.80
Implantation Sites			
Number of implantation sites (n)	18.6 ± 1.1	18.1 ± 0.9	0.74
Lengt (cm)	21.6 ± 1.7	23.2 ± 1.1	0.49

[a] Excluding one sow with 31 CL but only 3 (viable) embryos and 4 implantation sites

[b] Corrected for age at slauther

Table 6.4 LH characteristics per treatment for pregnant sows on day 14.3 ± 0.6 after insemination (LSmeans ± SEM)

	Control	Plus Feed	P value
Number of sows (n)	10	12	
Average (ng/mL)	0.68 ± 0.04	0.71 ± 0.03	0.57
Basal (ng/mL)	0.38 ± 0.02	0.34 ± 0.02	0.18
Number of pulses per 10 hours (n)	1.92 ± 0.26	2.25 ± 0.23	0.34
Pulse amplitude (ng/mL)	1.68 ± 0.19	1.89 ± 0.17	0.42
Average pulse area (ng/mL)	6.14 ± 0.47	6.40 ± 0.42	0.68
Total pulse area (ng/mL)	11.54 ± 1.44	14.05 ± 1.30	0.21

3.4. Metabolic parameters

Preprandial concentrations of glucose and insulin at day 15 were not different between Plus Feed and Control sows (82.1 ± 1.4 vs. 81.8 ± 1.2 mg/dL and 13.5 ± 1.6 vs. 14.7 ± 1.4 μIU/mL, respectively), and neither were the postprandial glucose profiles (Fig. 6.3A). Insulin peaked later (48 vs. 24 m after feeding) and at a higher concentration in the Plus Feed group compared with the Control group (115.5 ± 7.3 vs. 92.0 ± 9.5 μIU/mL, respectively, Fig. 6.3B). AUC for glucose tended to be lower for the Plus Feed than for the Control group (-171 ± 448 vs. 1257 ± 579 mg/6.2 h, respectively, P = 0.06). Area under the curve for insulin was not different between Plus Feed and Control sows (10 196 ± 854 vs. 7963 ± 1101 μIU/6.2 h, respectively, P = 0.12).

The IGF-1 concentrations were highest from days -1 to 6, after which they declined till day 17 of pregnancy after which they stabilized (Fig. 6.4A). Average IGF-1 concentrations were not different between treatments (151.6 ± 6.0 vs. 146.7 ± 7.8 ng/mL for Plus Feed and Control, respectively, P = 0.62). The NEFA concentrations decreased from d -1 to d six after which they stabilized (Fig. 6.4B). Average NEFA concentrations were lower for the Plus Feed group compared with the Control group (149.5 ± 9.2 vs. 182.4 ± 11.9 _m/L, respectively, P = 0.04). A negative correlation between weight gain from days 0–14 and average NEFA concentration was found (r = -0.45, P = 0.01, n = 31). Urea declined from days -1 to 6 after which it stabilized (Fig. 6.4C). Average urea concentration was higher for Plus Feed compared with Control sows (4.3 ± 0.1 vs. 3.9 ± 0.1 mmol/L, respectively, P = 0.03). This difference, however, disappeared after correction for pretreatment (day -1) urea concentration (4.3 ± 0.1 vs. 4.1 ± 0.1 mmol/L, respectively, P = 0.13). Urea concentration was negatively correlated with average progesterone concentration from days 11–15 (r = -0.42, P = 0.03, n = 25). Furthermore, urea concentration was positively correlated with average LH and total LH pulse area at day 14 of gestation (r = 0.51, P = 0.02, and r = 0.59, P = 0.01, respectively, n = 19). None of the metabolic parameters were related with ovulation rate, luteal weight, embryonic or placental characteristics.
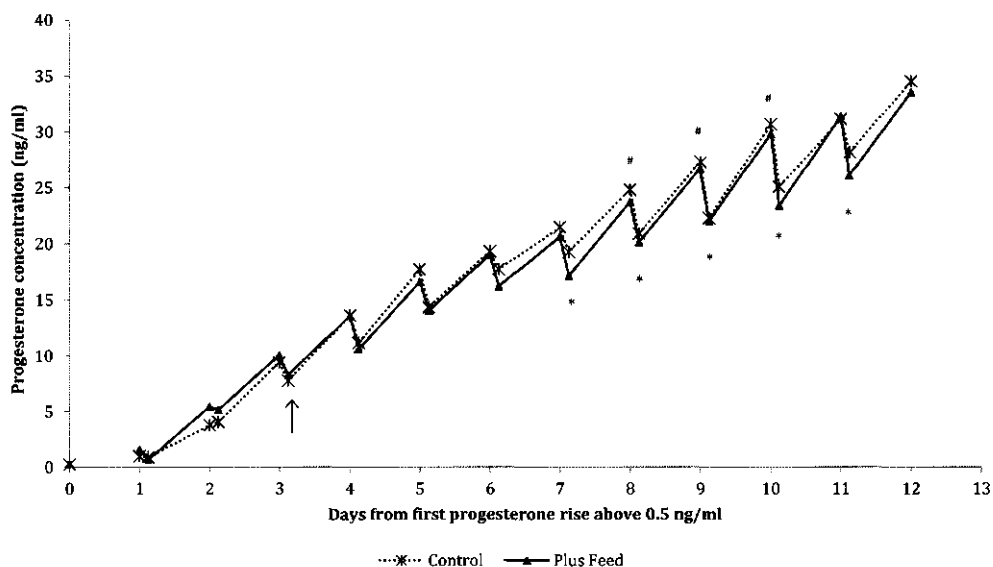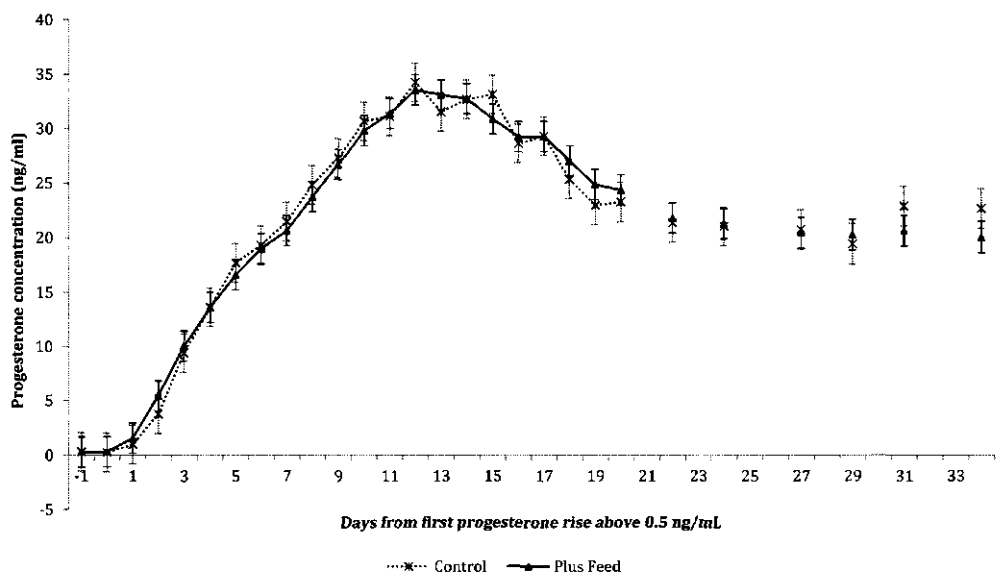
Figure 6.2 Progesterone profiles for pre-prandrial and 3h post-prandial samples for pregnant sows for Control (SEM 1.56) and Plus Feed (SEM 1.22) sows
Day 0 = first rise of progesterone above 0.5 ng/mL and a steady rise thereafter.
*   indicates a significant decrease in pre- vs. post-prandial progesterone in Plus Feed sows
#   indicates a significant decrease in pre- vs. post-prandial progesterone in Control sows.
    Arrow indicates, start of feeding treatment.

4. DISCUSSION

In gilts it has been repeatedly shown that high feeding levels are associated with lower embryonic survival (Jindal et al., 1996; Jindal et al., 1997; De et al., 2009). In multiparous sows negative effects of increased feeding level on embryonic survival are not found (Varley and Prime, 1993; Virolainen et al., 2005b), while effects in specifically second parity sows are hardly investigated. Second parity sows, sows weaned from their first litter, are still growing to achieve mature body size but often suffer substantial body reserve losses during first lactation. Therefore, restoration of body reserves is needed. A high(er) feeding level during early pregnancy might facilitate this restoration, however, it might also affect embryonic survival as shown in gilts. A recent study by Hoving, et al. (2011) showed that first and second parity sows fed a 30% higher feeding level during the first month of pregnancy, similar to current study, had a significant higher subsequent litter size (+2 piglets) from first insemination compared to control sows. Furthermore, even though litter size was increased, piglet birth weight was similar for both groups indicating an improved embryonic or placental development, or both. The current study was undertaken to find a physiological explanation for the effects on litter size as reported by Hoving, et al. (2011), and to describe reproductive and metabolic responses in first parity sows fed different feeding levels during days 3–35 of second gestation.

4.1. Embryonic survival, embryonic and placental development

A positive effect of high feeding level on litter size at term might be associated with an increased embryonic survival up to day 35 of pregnancy, or, if effects on embryonic survival are absent, a better embryonic and placental development and therefore increase the survival chances of the fetuses up to term. In current study, however, feeding 30% more feed did not affect embryonic survival or embryonic and placenta development at day 35 of pregnancy in second parity sows. Embryonic survival in our study was 73%, representing 15.8 viable embryos on day 35 of gestation. Further fetal losses are expected, since the peak of prenatal losses lies around day 50 of pregnancy (Vonnahme et al., 2002; Town et al., 2005). Prenatal survival after day 30–50 is predominantly related to placental development (reviewed by Vonnahme, et al. 2002). In our study, placental length and weight were not affected by treatment and it therefore does not seem likely that a difference in litter size and/or piglet birth weight would develop in these sows during the remainder of pregnancy.

4.2. Progesterone and LH

Negative effects of feeding level on embryonic survival in gilts have been explained by associated effects of feeding level on systemic progesterone concentration in early pregnancy. Several authors show that embryonic survival is mainly affected by progesterone concentrations during the first days of gestation (days 0–3, Pharazyn et al., 1991; up to

day 10, Van Den Brand et al., 2001a). An increased feeding level (4 kg or 2.0 x maintenance), however, can lower progesterone concentrations during early pregnancy in gilts (Jindal et al., 1996; Virolainen et al., 2004; De et al., 2009) and thereby reducing embryonic survival (Jindal et al., 1996; Jindal et al., 1997). In the current study, progesterone profiles and average progesterone concentration from days 1 to 10 were not different between treatments and were not related to embryonic survival rates. In multiparous sows a high feeding level also did not affect progesterone concentrations or embryonic survival (Kirkwood et al., 1990; 3.6 vs. 1.8 kg/day; Varley and Prime 1993; 3.5 vs. 1.5 kg/day; and Virolainen, et al. 2005b; 4.0 vs. 2.0 kg/day). The absence of effect of feeding level on systemic progesterone concentrations might explain why embryonic survival is not affected by feeding level in current study and in studies in multiparous sows. Consistent with results in gilts, reported by Virolainen, et al. (2005a) and Athorn, et al. (2011), our study shows the existence of a post-prandial decrease in progesterone concentrations which has been related to a post-prandial increase in metabolic clearance rate (Prime and Symonds, 1993).

Figure 6.3 Glucose (3A, SEM 2.42 for Control and 2.115 for Plus Feed) and insulin (3B, SEM 8.65 for Control and 7.56 for Plus Feed) profiles on day 15.3±0.6 after insemination.
Arrow indicates time of feeding (T = 0).
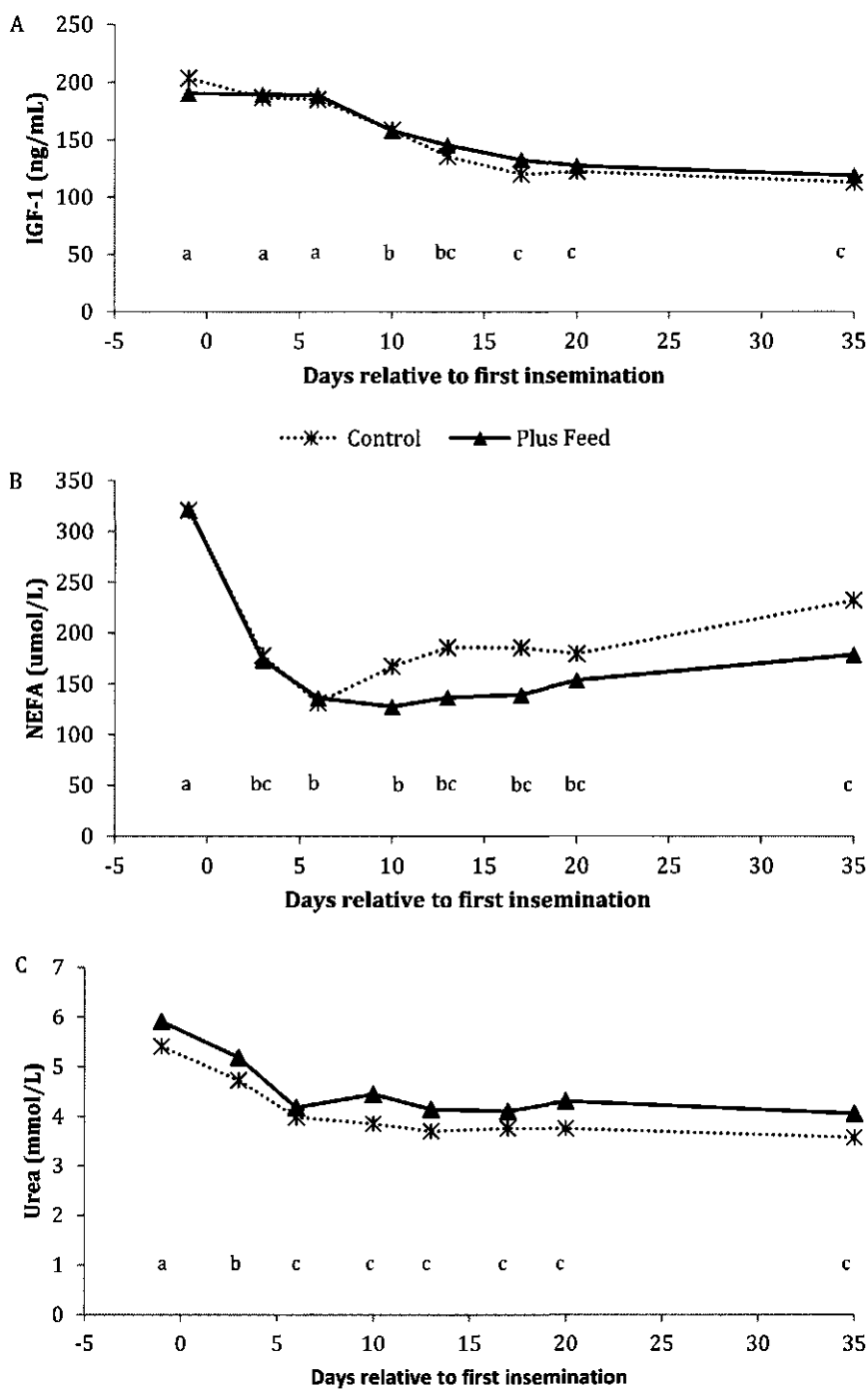* indicates significant difference between control and plus feed sows.

Figure 6.4 IGF-1 (A), NEFA (B) and Urea (C) profiles from d-1 till 35relative to first insemination) per treatment for pregnant sows1.

Samples are taken about one h before the morning meal; a, b, c indicate significant differences between d.
1 SEM for Control and Plus Feed sows, respectively, 10.1 vs. 7.7 (IGF-1), 19.39 vs. 15.25 (NEFA) and 0.20 vs. 0.16 (Urea)

In our study, the post-prandial decrease in progesterone, 3 h post feeding was significant from days 7–11 of gestation in the Plus Feed group and from days 8–10 of gestation in the Control group. Post-prandial progesterone concentrations, however, were not related to embryonic survival or development. Progesterone concentrations from days 12–29 of gestation have been reported to be dependent on LH secretion (Peltoniemi et al., 1995; Tast et al., 2000), an increased LH secretion could therefore positively influence progesterone concentration. Peltoniemi et al. (1997) reported that restricted feeding (1.8 vs. 3.6 kg/ day) in pregnant gilts negatively influenced LH pulsatility in winter, when reproductive performance is often suboptimal, Booth et al. (1996) reported similar results in prepubertal gilts (maintenance vs. ad lib feed allowance). We therefore hypothesized that an increased feeding level might increase LH pulsatility, and thereby progesterone concentration. In our study, however, feeding level did not affect LH characteristics on day 14 of gestation and these characteristics were not related to any of the embryonic or placental characteristics at day 35 of gestation. We did, however, find a negative correlation between basal LH concentration at day 14 and average progesterone concentration at days 11–15, suggesting that progesterone levels are sufficiently high to exert a negative feedback on LH, rather than LH positively affecting progesterone as has been described in literature (Peltoniemi et al., 1995; Tast et al., 2000). In conclusion, in the current study no evidence was found that progesterone or LH or both were affected by feeding level during early second pregnancy, either were their levels related with embryonic survival.
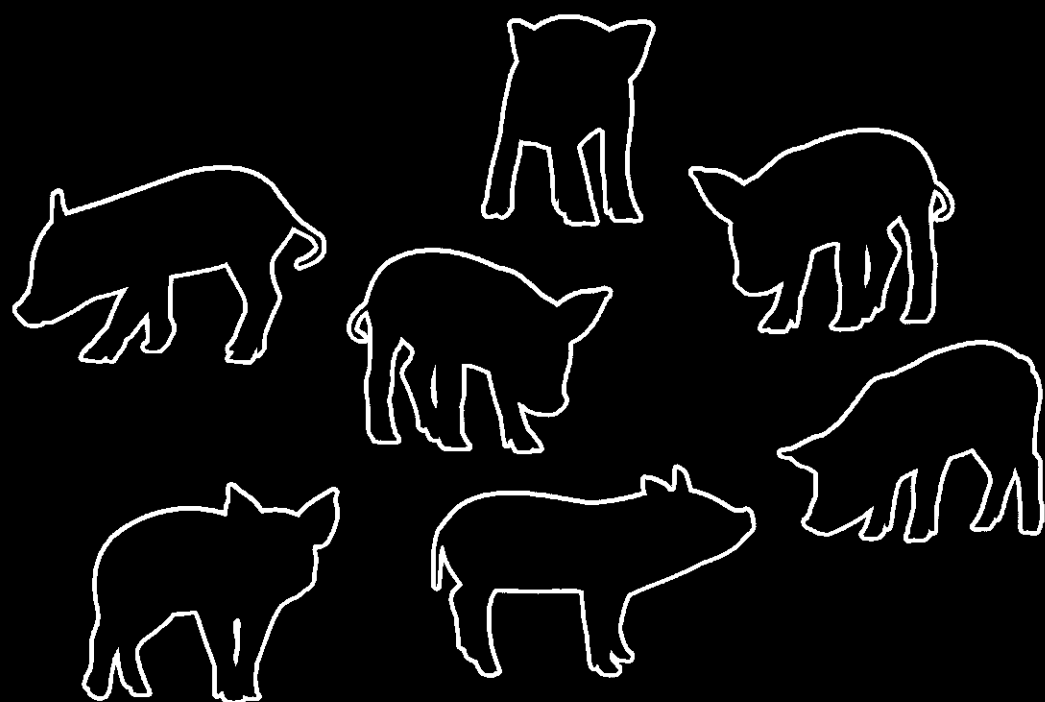
4.3. Sow development and metabolic hormones

Plus feed sows gained 5.4 kg more weight and 0.9 mm more back fat during the treatment period compared with Control sows. Similar results were found by Hoving, et al. (2011). In the current study the difference in weight gain was predominantly achieved during the first 14 days of treatment, indicating that the higher feeding level facilitates growth especially in the early period after weaning. Interestingly, ad libitum fed compared to restricted fed pregnant sows have a higher feed intake, and consequently, a larger weight gain in specifically the first 56 days of pregnancy and less so at later stages of pregnancy (Van Der Peet-Schwering et al., 2004). This result, as well as our finding, seem to make physiological sense, since the first possibility for sows to restore their lactation body weight losses is during early gestation (Dourmad et al., 1996). To our knowledge only a few authors have studied effects of feeding level on insulin and IGF-1 in early pregnancy. During lactation and weaning to insemination interval, a higher feed intake has been related to higher insulin and IGF-1 concentrations, which, in turn, have been related to gonadotropin release (Quesnel and Prunier, 1998; Wientjes et al., 2012). During gestation, De et al. (2009) reported increased insulin and IGF-1 concentrations on days 12, 25, and 35 of pregnancy in gilts fed 2 x maintenance compared to gilts Fed 1.2 or 0.6 x maintenance. IGF-1 has been related to increased progesterone production in luteal cells in vitro (Yuan and Lucy, 1996; Barb et al., 2001) and to an increased progesterone rise 12 to 36 h after ovulation

in vivo (Langendijk et al., 2008). We therefore, hypothesized that a higher feeding level would stimulate insulin and IGF-1 release during early gestation and thereby stimulate progesterone release, possibly partly though stimulated LH release. Furthermore, IGF-1 has also been reported to directly influence embryonic development around elongation and estrogen production around maternal recognition of pregnancy (Simmen et al., 1993) and there are indications that this might be influenced systemic IGF-1 (Simmen et al., 1998). An increased IGF-1 concentration could therefore directly influence embryonic development. The higher feeding level in current study did result in a higher post-prandial insulin peak at day 15 of pregnancy, but no relations were found between day 15 insulin parameters and day 14 LH characteristics, early gestational progesterone, IGF-1, NEFA, urea and day 35 embryonic and placental characteristics. Further, IGF-1 concentrations during the first month of pregnancy were not affected by feeding treatment and also not correlated with progesterone or other reproductive and metabolic parameters (results not shown). In lactating catabolic sows, liver IGF-1 release can be increased by increasing insulin concentration (Van Den Brand et al., 2001b) and is associated with LH pulsatility around weaning (Van Den Brand et al., 2001b) and basal LH during days 3–5 after weaning (Wientjes et al., 2012). This positive effect of insulin on IGF-1 could be due to the uncoupling of the growth hormone (GH) – IGF-1 axis in catabolic sows (reviewed by Quesnel (2009)) and dairy cattle (Lucy, 2008). However, in anabolic sows, like the sows in our study, liver IGF-release is mainly related with GH and not with insulin. Besides possible effect of insulin or IGF-1 concentrations or both on embryonic survival or development through ovarian stimulation of progesterone release, IGF-1 concentrations may also directly stimulate embryo development at a uterine level. Since both insulin and IGF-1 were not related to day 35 embryonic and placental characteristics, current study shows no (in)direct positive effect of these metabolites on embryonic development. The NEFA and Urea concentrations depend on the metabolic state of the sow. The NEFA are a product of fat metabolism and weight loss during lactation has been related to increased NEFA concentrations in sows (Hultén et al., 2002b; Valros et al., 2003). In dairy cattle, high NEFA have been associated with reduced embryonic development, either by affecting follicle development or by acting on the uterine environment or both (Leroy, 2005). However, dairy cattle are in a negative energy balance (i.e., showing high NEFA concentration) at time of insemination and during early pregnancy, while in most sows NEFA concentrations decrease to anabolic levels around one week after weaning (Yang et al., 2000; Hultén et al., 2002a). The relatively low concentration of NEFA are therefore unlikely to affect the uterine environment in sows. In the current study, during the first month of gestation, NEFA were lower for Plus Feed sows compared with Control sows and urea tended to be higher. Although back fat gain was not different between both groups, one could speculate that Control sows use body fat reserves to regain protein reserves. Plus Feed sows, in turn, use energy and amino acids from the feed to regain (protein) body reserves, as is indicated by the numerically higher urea concentration in these sows. Since urea is a product of protein metabolism, the numerically higher urea concentration in the Plus Feed sows may also be related to the higher protein

intake, as has been shown for lactating sows by Yang, et al. (2000) and Meija-Guadarrama, et al. (2002). In the current study, urea was positively correlated with average LH and total pulse area on day 14 of gestation. Positive correlations of urea and LH release have also been reported by Yang, et al. (2000) (r - 0.30–0.58), however, a physiological explanation or mechanism has not been found. Since neither NEFA nor urea were related to embryonic or placental development, the importance of these metabolites for reproduction in early gestation seems limited. The current study shows that a 30% higher feeding level facilitates body weight recovery and decreased NEFA concentrations during the first month of second gestation. However, feeding level did not affect embryonic and placental development, progesterone profiles or LH release. In addition, metabolic parameters were not affected by feeding level and were also not related with embryo and placental development. This experiment, therefore, fails to find a physiological explanation for the large effects on litter size in second parity sows found by Hoving, et al. (2011) but emphasizes that a higher feeding level in these sows during early gestation does not negatively affect embryonic survival as has been repeatedly reported for gilts. Increased feed intake during early second gestation can therefore improve sow development and might thereby increase sow longevity without negatively affect reproductive performance.
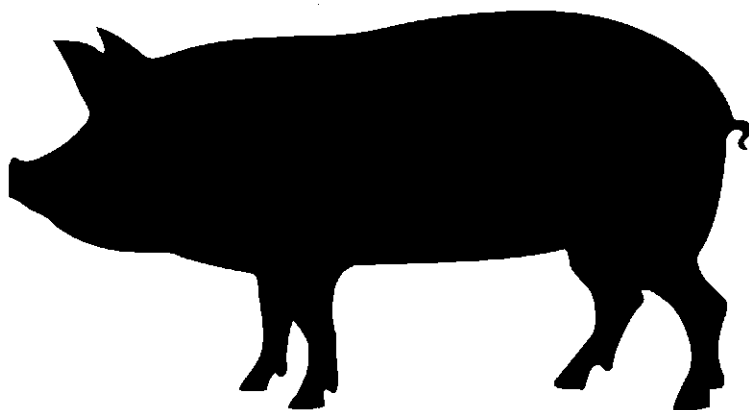
Chapter 7

General discussion

Litter size and farrowing rate are important determinants of sow reproductive performance and farm reproductive efficiency. Both farrowing rate and litter size usually increase as parity increases, reaching the highest levels from parity 3 to 5 (Koketsu et al., 1999; Hughes and Varley, 2003). However, second parity sows, i.e. sows of which their first litter is weaned, frequently show an equal or smaller litter size compared with their litter size in first parity (Chapter 2 & 4). Besides an equal or smaller litter size, a reduced farrowing rate or a high percentage of sows returning into oestrus after insemination can also be indicative of suboptimal reproduction in second parity as is shown in Chapter 2 and 4 of this thesis. Suboptimal reproductive performance in second parity sows negatively affects second parity reproductive performance, but it has also been related to a reduced reproductive performance in subsequent parities and to earlier culling of sows (Chapter 4).

In literature, many studies report that high weight loss during lactation, especially in primiparous sows, are related to reduced embryonic survival, litter sizes and farrowing rates (Clowes et al., 2003a; Thaker and Bilkei, 2005; Schenkel et al., 2010; Chapter 2 and 3). The increased litter size over the last decade, from 11.2 to 13.3 live born piglets (Agrovision BV, Deventer, The Netherlands), has increased the metabolic demands for milk yield during lactation. Feed intake, however, did not increase sufficiently and is often limited to fulfil the metabolic demands for of the sow (Eissen et al., 2003; Bergsma, 2011). If energy output (milk yield and maintenance costs) is higher than energy input (feed intake), sows use their body reserves to ensure milk production, which induces weight loss. The focus of breeding programmes on grower and finisher traits or lactation efficiency, might lead to an even larger decrease of voluntary feed intake, which might increase weight loss even further (Bergsma, 2011). With increasing lactation weight losses, prevalence of suboptimal reproduction, especially in physically immature (second or third parity) sows, may also increase. As a consequence, sow longevity can be reduced, since reduced reproductive performance is one of the main culling reasons in young sows (Lucia et al., 2000).

In the following paragraphs results obtained in this thesis will be discussed. Paragraph 7.1 discusses the extent to which suboptimal second parity reproduction can be regarded a problem for farm productivity, as well as some considerations that should be taken into account when evaluating second parity reproductive performance. Paragraph 7.2 discusses the effects of lactation weight loss on metabolic parameters and second parity reproductive performance. Paragraph 7.3 discusses several preventive measures and possible tools to reduce the negative effects of lactation weight loss on reproduction. In paragraph 7.4 the association of an increased feeding level during early second gestation with subsequent reproductive performance, metabolic changes and sow development is discussed. To conclude, practical recommendations for pig husbandry and conclusions are given in paragraph 7.5 and 7.6, respectively.

7.1 Extent of the problem

As is mentioned above, litter size and farrowing rates usually increase up to parity 3 to 5. Therefore, besides having a lower litter size, having an equal litter size in parity 2 vs. 1 can also be an indicator for suboptimal reproductive performance in second parity. Having an equal or lower litter size in second parity can be defined on farm level: i.e. the average litter size of all sows in second parity is equal or lower than the average litter size of all sows in first parity, but also on sow level; i.e. litter size in second parity is equal or lower than litter size in first parity. Farm level estimates of equal or lower second parity litter size vary from 50% (53/106, Saito et al., 2010), to 40% (49/122, Morrow et al., 1992) and 12% of the farms (10/85, our data). Estimates of equal or lower second parity litter size on sow level are more consistent and vary around 50% (54% Morrow et al., 1992), 49% Saito et al., 2010) and 51% Chapter 4).

When evaluating litter size in second parity, it is important to evaluate litter size from first insemination, i.e. insemination(s) in first cycle after weaning [Chapter 4], since repeat breeders often show higher litter sizes compared to sows that farrow from first insemination after weaning (Tummaruk et al., 2001b, Figure 7.1). Reduced litter sizes can therefore be masked, especially on farms with a high percentage of repeat breeders.

Estimates of farrowing rates on farm level per parity are scarce. Data from Chapter 4 showed that on 56% (48/85) of the farms, farrowing rate in second parity was lower than in first parity, whilst in total 15.7% of the second parity sows were repeat breeders.
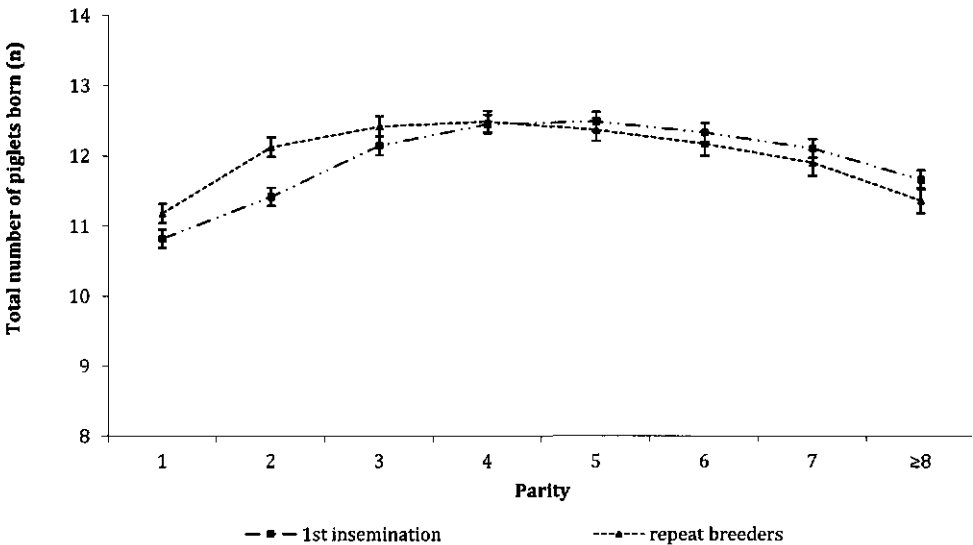

Figure 7.1 Total number of piglets born per parity for repeat and non-repeat breeders, adapted from data from chapter 3.

The extent to which reduced second parity reproduction can be experienced as a problem depends if you study it from a farm level or sow level perspective. If, on farm level, average second parity litter size or farrowing rate is reduced compared with first parity, probably everyone would agree that there is a problem with reproductive performance in second parity sows, provided that there is sufficient data available. However, when litter size or farrowing rate on farm level increase from first to second parity, and only a proportion of second parity sows show reduced reproduction, one can argue whether or not there is a problem.

Ten of the studied farms used in Chapter 4 had an equal or lower litter size in second parity than in first parity on farm level (Figure 7.2). On these farms, a high percentage of sows (≥55%) showed an equal or lower litter size in second compared with first parity. On farms where litter size increases from first to second parity, however, also 45-55% of the sows showed a smaller litter size in second parity compared with first parity (Figure 7.2). Thus, even though average litter size from first to second parity increases and, on average there might not be a problem with second parity litter size, a high percentage of sows can still show suboptimal litter sizes in second parity compared with first parity. Improving litter size in these sows will therefore increase farm reproductive performance (Sasaki and Koketsu, 2008) and also farm productivity. As shown in Figure 7.3 the difference between litter size in first and second parity tends to be more related with second parity litter size (triangles, solid line, r = 0.23, P = 0.06) than with first parity litter size (no data points, dotted line, r = -0.17, P = 0.18). One could therefore conclude that improving second parity litter size, rather than improving first parity litter size, will improve farm productivity. However, the correlations are low and inferences from these relation should be made with caution.

On sows level, litter size in first and second parity show a low correlation (r = 0.27, P = <0.0001, Figure 7.4), which makes it more difficult to use 'reduced reproductive performance' as a measure of reproductive succes for individual sows. On sow level, the definition 'reduced second parity litter size' is highly dependable on litter size in first parity (Morrow et al., 1992, Chapter 4) and to a large extent a result of 'chance'. For example, a first parity sow with 16 piglets born alive has a higher chance to have a reduced litter size in second parity compared to a first parity sow with only 10 piglets born alive, since a litter size of 16 piglets is more difficult to improve than a litter size of 10 piglets.

In conclusion, the use of 'reduced litter size' in second parity compared with first parity can give an indication of farm reproductive efficiency. On sow level, however, 'reduced litter size' is a highly variable trait and to a large extent determined by chance. Absolute litter sizes are therefore a better indicator of second parity sow performance.
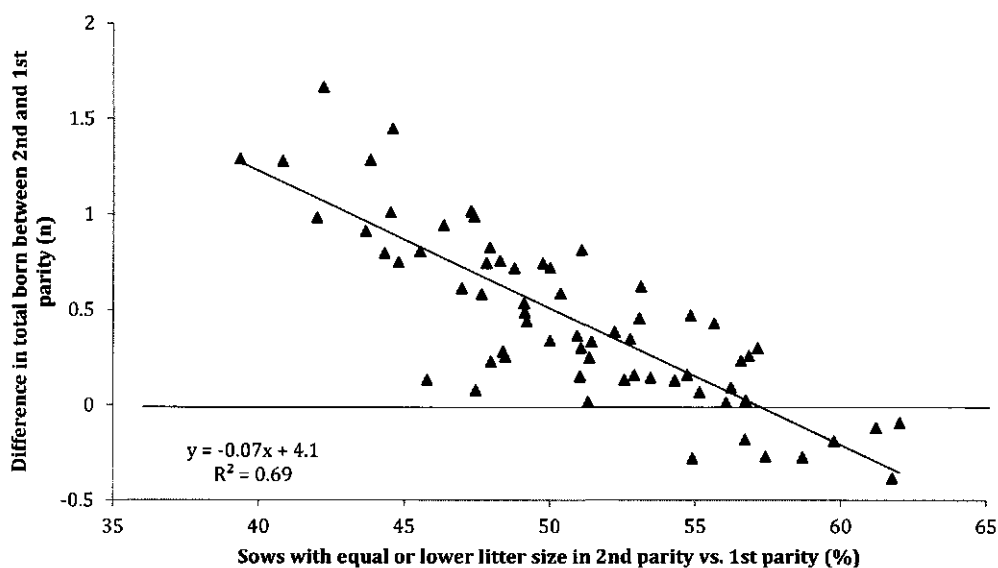
Figure 7.2 Relation between difference in 2nd and 1st parity litter size and the number of sows with a reduced litter size in 2nd compared with first parity. Data from chapter 4 for farms with > 100 observations. The horizontal bar represents a difference of 0 between 2nd and 1st parity litter size.
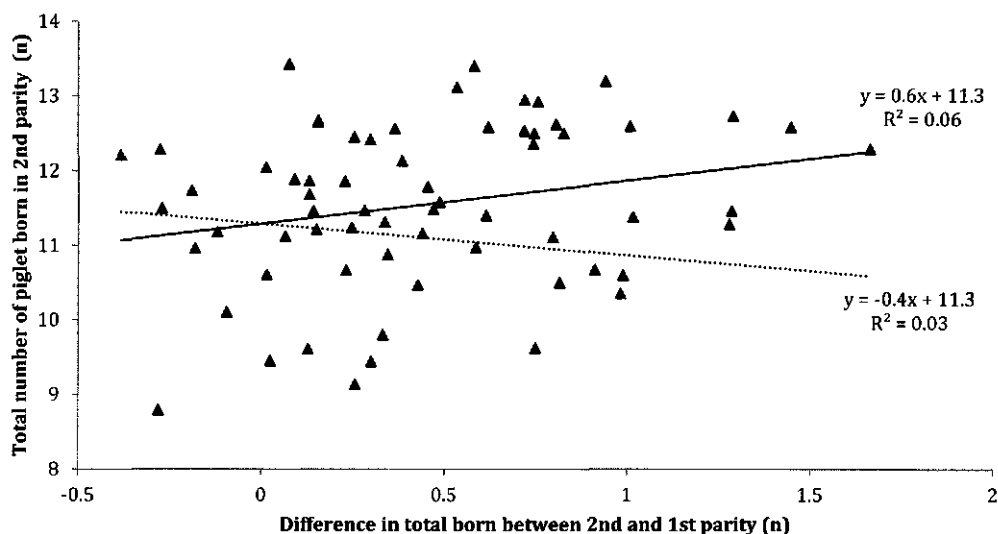

Figure 7.3 Relations between the difference between 1st and 2nd parity litter size on farm level and total number of piglets born in second parity (solid line) and first parity (dotted line).
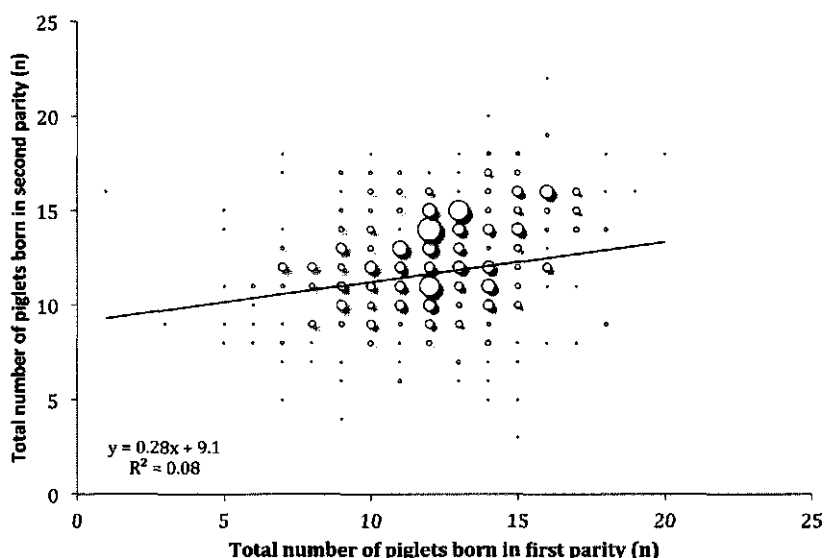
Figure 7.4. Relation between litter size in first parity and litter size in second parity on sow level (n = 430) for a randomly selected farm (Data from chapter 4). Solid line represents the trend line. Area of the bubbles represents the number of observations, varying from 1 to 15).

Considering the above, we decided to relate absolute litter sizes in second parity, rather than 'reduced litter size in second compared with first parity', to litter sizes in later parities. Little information is available on the relation between second parity reproductive performance and reproductive performance in later parities. If there is a positive relation, improving second parity reproductive performance will not only benefit farm productivity by improving second parity litter size, but also by improving reproductive performance in later parities. As is reported in Chapter 4, litter size in parity 3 and up is lower for sows that had a low litter size in second parity (≤10 piglets born total) than for sows with a high second parity litter size (≥ 14 piglets total born). However, the extent of the decrease depends on litter size in first parity. Sows with a low second parity litter size and a low first parity litter size produced 3.3 piglets less in parity 3 to 5 than sows with low second parity litter size but a high first parity litter size (34.2 ± 0.4 vs. 37.5 ± 0.4 total born piglets, respectively). It was therefore concluded that only litter size in second parity is not a good indicator for future sow productivity and that the sum of litter size of first and second parity litter size would be a better indicator. In accordance with our study, Sasaki et al. (2011) reported that the summed litter size in first and second parity is a good indicator of future sow reproductive performance. In their study, sows with a high summed number of piglets born alive in first and second parity (average 26.7 ± 0.02, n = 11,597) produced 7.8 alive piglets more in parity 3-5 (35.9 ± 0.03 vs. 28.1 ± 0.03, respectively) and were culled 0.5 parity later (5.7 ± 0.02 vs. 5.2 ± 0.02, respectively) than sows with a low summed number of piglets born alive in first and second parity (average 13.4 ± 0.02, n = 10,958).

Similarly, data from Chapter 4 also show that sows with a high litter size in both first (≥13 piglets born total) and second (≥14 piglets born total) parity produced 6.6 more piglets in parity 3-5 than sows with a low litter size (≤10 piglets born total) in first and second parity (40.8 ± 0.4 vs. 34.2 ± 0.4, respectively). Therefore, reproductive performance in the first two parities could be considered as a selection tool for highly productive sows, provided that economic calculations show a positive effect on farm economics.

The relation between litter sizes in first and second parity and litter sizes in later parities can be due to genetic differences in reproductive potential, but can also be due to (genetic) differences in the ability to cope with a suboptimal environment. For example, Bloemhof et al. (2008) reported differences in heat stress tolerance, measured by reproductive performance, between two sow lines. In practise this might mean that some sows are able to maintain a sufficiently high feed intake during high environmental temperatures in the farrowing room, whilst others are not. As a result, weight loss of the former sows might be lower and their reproductive performance higher than the latter sows. Optimal farm management based on individual sows, however, might reduce differences between sows, as is illustrated by the high correlation ($r = 0.91$, $P < 0.0001$) between first and second parity litter size on farm level (Figure 7.5). Furthermore, the effect of first parity litter size on subsequent reproductive performance might also be due to the long lasting effects of gilt management on sow development (Challinor et al., 1996; Tummaruk et al., 2001a). Gilt rearing and gilt breeding strategies determine, for a large part, first parity litter size but also determine sow body development and thereby the ability of a gilt to withstand weight losses during first lactation (Paragraph 7.3).
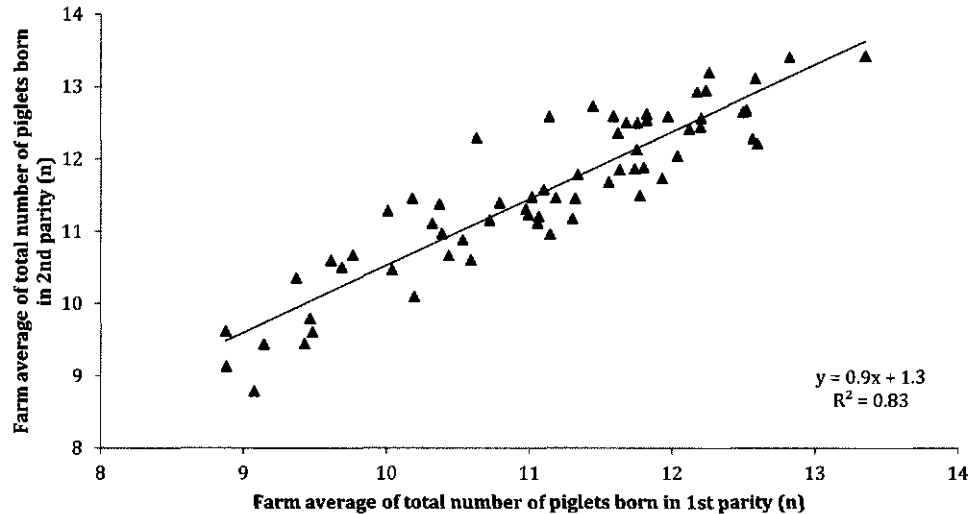

Figure 7.5 relation between litter size in first and second parity on farm level.
Data from chapter 4 for farms with >100 observations.

7.2 Lactation weight loss

A large number of studies have reported negative consequences of feed or protein restriction and weight loss on sow metabolism and subsequent reproductive measurements, e.g. weaning to oestrus interval (WOI), follicle and oocyte quality, embryonic survival and farrowing rate or litter size (Table 1.1, Chapters 2 and 3). In most of these studies, severe feed or protein restriction is used as a model for lactation weight loss and sows are often fed at or just above maintenance levels. In practise, however, lactating sows are fed well above maintenance or even at ad libitum levels and weight losses are based on variation in voluntary feed intake, milk production and costs for maintenance. Effects of weight loss on reproductive functioning and metabolism might therefore be different during severe feed restriction than if feeding levels are close to ad libitum. Furthermore, most studies only focus on metabolic changes during lactation without exploring possible carryover effects of these metabolic changes into early gestation. If metabolic changes from lactation are continued into early gestation, they can also influence embryonic survival or development during early gestation, and perhaps litter size at term. Results in Chapter 3 were therefore obtained from sows fed according to lactation feeding schemes used in practise and metabolic changes were measured from the last 10 days of the first lactation up to day 35 of second gestation, to give more insight in relations between metabolic parameters in lactation and subsequent gestation.

7.2.1 Metabolic changes during and after lactation and their relation with reproduction
During lactation, energetic demands for milk yield and maintenance are often higher than energy supply by feed intake and sows therefore use their body reserves as an energy and protein source for milk production (Eissen et al., 2000). This so called negative energy balance (NEB) is accompanied by several distinct metabolic and hormonal changes (Table 7.1), which, in turn, can influence subsequent reproductive performance. The effects of weight loss on the measured metabolic parameters in Chapter 3 were similar compared with results found in the literature (Table 7.1). However, the differences between high and low weight loss sows were less pronounced in our study compared to literature, which might indicate that metabolic parameters are less influenced by (severe) weight loss when feed supply is approaching ad libitum levels, than when feed or protein supply are restricted.

In pigs, Insulin like Growth Factor-1 (IGF-1) is one of the most intensively studied metabolic hormones which is related to lactation weight loss (Table 7.1), but also with follicle and oocyte development and reproductive performance. IGF-1 concentrations can influence follicle development during and after lactation either directly by increasing the follicular response to gonadotropins (Quesnel, 2009), or indirectly by acting on the hypothalamus and thereby influencing pulsatile LH release by the pituitary (Quesnel and Prunier, 1998; Van Den Brand et al., 2001b). Concentrations of IGF-1 decrease when sows are in

Table 7.1 Change in metabolic parameters for sows in a negative energy balance

Metabolic parameter	No Treatment[*]	Ref[**]	Feed Restriction[#]	Ref[**]	Protein Restriction[#]	Ref[**]
Insulin	Stable	1	Not different	6	Lower	4
			Lower	3		
IGF-1	Lower	1, 8	Lower	5, 6	Lower	4
Growth Hormone	Increase	1	Higher	3	Higher	4
NEFA	Higher	1, 2, 8				
Leptin	Not different	8	Not different	7	Not different	4
Urea	Not different	1, 2, 8				
Creatinine	Not different	2	Higher	3, 9		

* change during gestation (ref 1) or difference between 'naturally' high or low weight loss sows (ref 2, 8)
** Ref = Reference; # restricted vs. non-restricted
1) Kraetzl et al., 1998, parity not clear; 2) Hultén et al., 2002a, multiparous sows; 3) Baidoo et al., 1992b, second parity; 4) Meija-Guadarrama et al., 2002, primiparous sows; 5) Brand et al., 2001b, primiparous sows 6) Zak et al., 1997a, primiparous sows; 7) De Rensis et al., 2005, mixed parity sows; 8) Hoving et al., Chapter 3, primiparous sows; 9) Park et al., 2008, multiparous sows

a negative energy balance (Table 7.1) and low IGF-1 concentration at the end of lactation can therefore negatively affect follicle and oocyte quality. Although IGF-1 concentrations during lactation were not significantly different between high and low weight loss sows in our study (Chapter 3), they were negatively correlated with lactation weight loss (r = -0.38) and lactation loin muscle loss (-0.48). Furthermore, regardless of lactation weight loss, sows with higher than average IGF-1 concentration during the last 10 days of lactation (> 143.5 ng/mL) had a higher number of vital embryos (17.3 ± 0.8 vs. 14.8 ± 0.8, P = 0.04) and tended to show a higher vital embryonic survival (77% vs. 67%, P=0.07), than sows with a lower than average IGF-1 concentration (≤ 143.5 ng/ml) during the last 10 days of lactation. This suggests that reduced IGF-1 concentration is (partly) responsible for the lower embryonic survival in sows with a high lactation weight loss. In lactating dairy cattle, NEFA concentrations are high and have been reported to affect embryonic survival. In lactating sows, NEFA are also related to weight loss (Table 7.1). However, their relation with reproductive performance is not clear, as is discussed in Chapter 3, in which no relations between NEFA concentrations during lactation and reproductive measures were found. Leptin and urea concentrations during lactation were not different between high and low weight loss sows (Chapter 3), as is also described in the literature (Table 7.1). Furthermore, in Chapter 3 no relations of leptin and urea with reproductive performance were found, which is similar to findings in the literature (De Rensis et al., 2005; Summer et al., 2009).
After weaning sows quickly shift into a positive energy balance, and metabolic changes that occurred during lactation are reversed (Chapter 3). However, lactation weight loss can still influence metabolic or hormonal profiles in the period directly after weaning, as reported by some authors (Kraetzl et al., 1998; Van den Brand et al., 2001a). Results from Chapter 3 showed that urea and IGF-1 were non-significantly lower on day 4 after weaning in high weight loss compared with low weight loss sows. This suggests a possible metabolic carry over effect from lactation, which may influence follicle development up to ovulation. Furthermore, Langendijk et al. (2008) reported that IGF-1 concentrations

shortly after ovulation are positively correlated with the rise of progesterone after ovulation in primiparous sows. In this thesis (Chapter 3), high weight loss sows reach their progesterone peak values 1.3 days later than low weight loss sows. Perhaps the lower IGF-1 concentrations during WOI in high weight loss sows negatively affected progesterone profiles either directly by affecting progesterone secretion by luteal cells or indirectly, by affecting luteinisation of follicles in the high weight loss sows (Ptak et al., 2003, 2004), causing a slower rise in progesterone which might have affected synchronic development of embryos and uterus (Foxcroft, 1997) and thereby embryonic survival.

From day 8 after weaning (~ day 3 after insemination) onwards concentrations of metabolic hormones were similar for both groups of sows, indicating that metabolic differences between high and low weight loss sows are not continued into (early) gestation.

7.2.2 Sow development and its relation with reproductive performance

High milk yield en relatively low feed intake capacity in current pig husbandry make weight losses during lactation almost inevitable. It is therefore important to consider to how much weight a sow can lose during lactation without negatively affecting reproductive performance. In literature, lactation weight losses up to 12% are considered 'safe' losses, without effects on subsequent reproduction (Clowes et al., 1998; Clowes et al., 2003a; Thaker and Bilkei, 2005; Schenkel et al., 2010). Results from this thesis also show negative effects of weight loss on being a repeat breeder (Chapter 2; odds ratio = 2.85 for weight loss of >15% vs. weight loss ≤15%), pregnancy rate (Chapter 3; 74% for weight loss of >13.8% and 96% for weight loss ≤13.8%) and embryonic survival. In Chapter 3, vital embryonic survival was lower for sows with a high weight loss (> 13.8%, based on the median of 48 sows) than for sows with a low weight loss (≤13.8%; 65.6 ± 3.4 vs. 77.4 ± 2.9%, respectively, P = 0.02). The median weight loss of 13.8% in Chapter 3 was chosen as a threshold value for low and high weight loss. This threshold value, however, did not represent a physiological threshold above which sows show a reduced embryonic survival (Figure 7.6). Figure 7.6 shows that the chances for low reproductive performance are increased if weight loss during lactation increases and reaches a certain threshold value. This threshold is more a range than a single value, therefore, in practise a weight loss of more that 10-14% should be avoided.

In scientific research, weight loss is a commonly used method to evaluate sow body condition development during lactation, whilst back fat measurements are commonly used under practical circumstances. Weight loss consists of protein, fat and water losses. Of these three, protein losses have been suggested to have the largest effects on weight losses (McNamara and Pettigrew, 2002) and reproductive performance (Clowes et al., 2003a). This suggests that protein loss rather than back fat depth loss should be measured as an indicator for the loss of body condition of the sow.
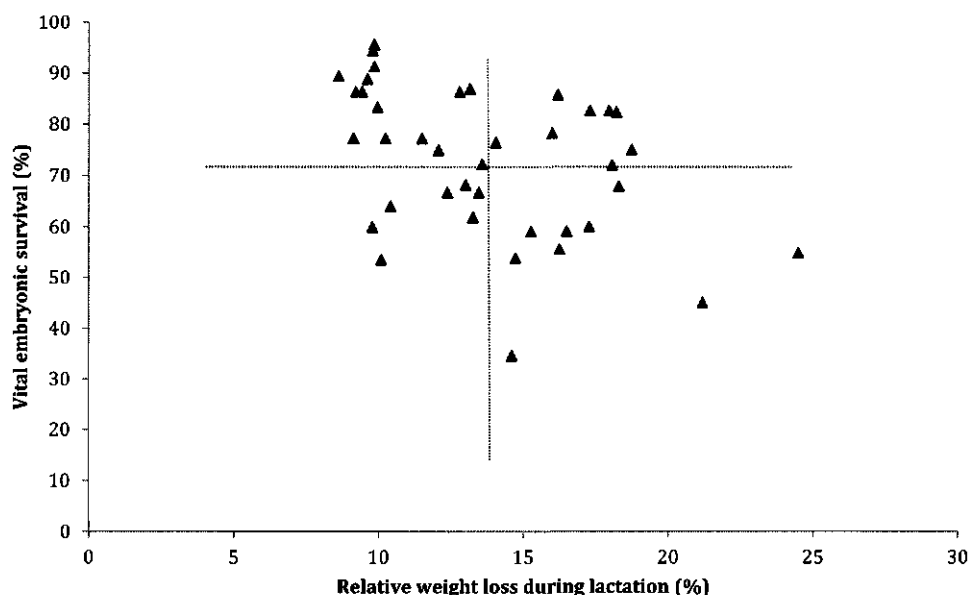
Figure 7.6 Relation between relative weight loss during lactation and vital embryonic survival at day 35 of gestation. The vertical line represents a relative weight loss of 13.8%, the horizontal line represent the average vital embryonic survival of 72%.

Using data from Chapter 3 and 5 we evaluated loin muscle depth as a measure for protein mass and back fat depth as a measure of fat mass and evaluated their relation with body weight development and reproduction. Weight loss indeed showed a high correlation with loin muscle depth loss ($r = 0.60$ and $r = 0.64$, respectively) whilst the correlation with back fat depth was low ($r = 0.15$ and $r = 0.29$, respectively), as was also described by Clowes (2001; $r = 0.64$ for weight and loin muscle depth and $r = 0.24$ for weight and back fat depth). Furthermore, significant correlations were seen between loin muscle depth and calculated protein mass ($r = 0.52$, data from Chapter 3) and back fat depth and calculated fat mass ($r = 0.60$, data from Chapter 3).These correlations were also similar to the correlations reported by Clowes (2001; $r = 0.49$ for loin muscle depth with protein mass and $r = 0.89$ for back fat depth with fat mass). One can therefore conclude that weight loss is more related to protein loss, as measured by loin muscle depth, than to fat loss, as measured by back fat depth. Loin muscle depth loss, however, only explains ~27% of the variation in protein mass loss, indicating that other muscle losses might be more important for weight loss.

Even though loin muscle loss was correlated with weight loss ($r = 0.60$) and IGF-1 ($r = -0.48$, data from Chapter 3), no relation between loin muscle depth and reproductive performance was found. This indicates that loin muscle depth loss is not a good predictor for subsequent reproductive performance. Furthermore, loin muscle depth measurements are variable and depend on which part of the muscle is measured. The measurements are

also very labour intensive and the equipment is costly, making them unfit for use in practise. Similarly to loin muscle loss, back fat loss also showed no relation with reproductive performance. Maes et al. (2004) reported no significant associations between back fat loss and weaning to insemination interval and a low association with back fat changes and litter size in subsequent parity. Concluding, weight loss is probably the best predictor for sow body condition loss and is related with subsequent reproductive performance. Weighing is therefore a practical and more accurate, tool to measure sow body condition development than back fat or loin muscle depth measurements.

7.3 Potential for improvement

The next paragraph will describe several management tools which can be applied to either gilt management (7.3.1), reduce lactation losses (7.3.2) or reduce the negative effects of lactation losses (7.3.3) in order to improve reproduction in second parity.

7.3.1 Gilt development from first insemination up to first weaning

Gilt age and development at first insemination are important determinants of reproductive performance in first and subsequent parities, as well as for sow longevity (Schukken et al., 1994; Challinor et al., 1996; Tummaruk et al., 2001a). Gilt management strategies are therefore important for farm efficiency. Current management strategies, however, are often based on research in older genotype sows. The modern genotype gilt is leaner with a lower appetite than its older counterpart and is therefore more sensitive for nutritional (miss)management (Bortolozzo et al., 2009). Gilt management strategies should therefore be adapted to fit the modern gilt. From their review on North-American gilt development strategies, Bortolozzo et al. (2009) conclude that gilts with a weight of 135-150 kg, and at least one previously recorded oestrus, can be inseminated regardless of age and back fat, with the prospect of good reproductive performance. Inseminating at a lighter weight decreases the number of life born piglets over three parities (Williams et al., 2005). Excessive body weight (>150 kg) and back fat depth should be avoided, since they increase the risk of culling due to locomotive problems (Bortolozzo et al., 2009). In contrast to North-American strategies, rearing strategies in the Netherlands use age, weight and back fat targets to ensure optimal gilt development at first insemination and first farrowing. The advised weight at first insemination (140 kg at 240 days of age, TOPIGS, Vught, The Netherlands), however, is similar compared to the weight at first insemination proposed by Bortolozzo et al. (2009). The main difference to achieve optimal weight at first insemination between both rearing strategies is therefore mainly due to growth rate. Other factors related to rearing conditions, for example space allowance or feed quality, will also affect gilt quality at time of first insemination. However, they fall out of the scope of this thesis and will therefore not be discussed further. To conclude, there is not one general rearing strategy that can be applied to all sow farms, since the optimal rearing strategy varies and is based on farm management strategies and sow breeds.

Besides growth during rearing, sufficient growth should also take place during first gestation, in order to achieve a body weight and composition that ensures good lactation performance, i.e. feed intake, milk production, etc. When body weight and body composition at first farrowing are suboptimal, lactational performance as well as reproductive performance in second parity can be negatively affected (Clowes et al., 2003b; Quesnel et al., 2005). For example, Clowes et al. (2003b) report that subsequent reproductive performance is less affected by protein loss in gilts with higher body mass at first farrowing compared with standard body mass at first farrowing. Furthermore, most studies on gilt management strategies focus on gilt growth and development up to first insemination or sometimes first farrowing. However, gilt growth and development up to first weaning might also be important. Results from Chapter 2 showed that an increased weight gain from first insemination up to first weaning increased farrowing rates in second parity on both farms. Furthermore litter size in second parity was positively affected by an increased sow development from first insemination to first weaning on the farm where gilts were lighter and younger at first insemination.

7.3.2 Reduce lactation losses

Weight losses during first lactation should be at most 10-14% to achieve good reproduction results in subsequent parities (7.2.2). Lactation weight losses can be minimized by either increasing feed intake during lactation or reducing the lactational burden.

7.3.2.1 Increasing Feed intake

Increasing feed intake during lactation is the most important factor in decreasing weight losses, especially since increased litter sizes make it difficult to reduce number of piglets suckling. Selection for lean genotype finisher pigs with a low feed conversion ratio, however, has decreased voluntary feed intake of lactating sows (Bergsma, 2011). Nevertheless, feed intake during lactation can often be increased by adjusting several environmental conditions. One important factor influencing feed intake is the temperature in farrowing rooms. The temperatures in farrowing rooms often exceed 20-23°C and are close to or above the upper critical temperature[2] (UCT , 22°C, reviewed by Makkink, 1998) of sows. If room temperatures rise above the UCT, sows reduce feed intake to prevent heat production (Black et al., 1993). Based on a review of 9 studies, Black et al. (1993) assessed that feed intake of sows decreases with 0.17 kilogram (2.4 ME DE) with every 1°C rise in environmental temperature above 16°C. Simply reducing farrowing room temperatures will therefore increase sow feed intake. However, low(er) room temperatures may negatively affect piglet performance, since the lower critical temperature[3] (LCT) for suckling piglets is around 30°C (Black et al., 1993). In practise, a balance should be found from which both sow and piglets benefit. Creating a warm micro climate for the piglets, for example by heating a designated area of the floor of the farrowing crate (Kuhn, 1990, cited from Makkink, 1998), results in high environmental temperatures for piglets and enables the farmer to lower the farrowing room temperature, which benefits the sow. One should keep in mind that

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[2] *The upper critical temperature is the temperature above which evaporative heat loss is increased in order to maintain a constant body temperature.*
[3] *The lower critical temperature is the temperature below which heat production increases in order to maintain a constant body temperature.*

the room temperature should be around 24°C or higher around farrowing, since new born piglets have minimal heat regulation capacity and are therefore at risk for hypothermia (reviewed by Makkink, 1998). Additionally, drip cooling, to increase evaporative heat loss (Makkink, 1998), and snout (McGlone et al., 1988) or floor cooling, to increase convection heat loss (Silva et al., 2006, 2009), are methods that can be used to decrease heat stress in lactating sows and thereby increase feed intake and even litter performance. Increasing the number of feedings per day and thereby decreasing the amount of feed per feeding, might also increase sow feed intake during periods of heat stress. Furthermore, feed intake is correlated with water intake (Kruse et al., 2011). In order to optimize feed intake, water should therefore be available ad libitum and water nipples should supply fresh water with a minimum rate of 2.5 l/min. Supplying cooled water of 10 to 15°C also increases feed intake and decreased rectal temperature in lactating sows compared with water of 20°C (Jeon et al., 2006).

7.3.2.2 Reducing lactational burden

Milk production is relatively low after farrowing but quickly increases as lactation progresses, reaching its peak around week 3 after farrowing (Noblet and Etienne, 1986; Daza et al., 1999). The amount of milk that is produced depends on several factors such as feeding level (Van Den Brand et al., 2000a) and the number and weight of suckling piglets (King et al., 1997; Auldist et al., 1998; Nielsen et al., 2002). Reducing the number of piglets, especially during the last week of lactation, might therefore decrease milk yield and reduce lactation weight loss. Furthermore, by reducing the suckling stimuli, LH pulsatility might also be restored, which might positively affect follicle growth up to weaning (paragraph 1.1.1). Two methods that can be used are split weaning; weaning part of the litter in the last week of lactation, and intermitted suckling; separating the sow and piglets for a few hours per day to reduce number of sucklings and stimulate piglets to eat creep feed. In their review, Soede et al. (2009) discuss both methods and conclude that both split weaning and intermitted suckling stimulate follicle development during lactation, but that the effects on weaning to oestrus interval are variable. Furthermore, effects of split weaning on weight loss are variable and depend on the regime used. For example, Vesseur et al., (1997) report that reducing litter size to 6 piglets during the last 7 days of a 28 day lactation, reduced lactation weight loss by 2-3% in first and second litter sows, whilst Zak et al (2008) showed no significant effects of reducing litter size to 4 piglets during the last 3 days of a 21 day lactation on weight loss. Perhaps the period of split weaning in the latter study was too short to affect lactation weight loss. Little information is available on the effects of intermitted suckling on sow weight loss. Kuller et al. (2004) report that weight loss was lower in sows of which the piglets were separated for 12 hours a day from day 12 to d 25 of lactation, than in sows of which the piglets were not separated during the 25 days lactation (9 ± 2.0 kg vs. 17 ± 2.0 kg, respectively). Furthermore, Gerritsen et al., (2008), also reported that weight loss was lower in sows that were separated from their piglets for 12 hours per day than in sows that were only separated for 6 hours per day.

Besides decreasing the number of piglets during late lactation, reducing lactation length can also prevent weight loss in lactating sows (Willis et al. (2003), 14 vs. 24 days; Koketsu et al. (1998), 12 vs. 21 days). However, lactation lengths shorter than 21 days negatively influence oocyte development, weaning to insemination interval and litter size and farrowing rates (reviewed by Soede et al., 2009). These negative effects are probably caused by an insufficient restoration of LH pulsatility during lactation, as is described in the introduction of this thesis, but can also be caused by an insufficient recovery of the uterus (Varley, 1982). In contrast to a shorter lactation length, increasing the lactation length from 3 or 4 weeks to about 5 to 6 weeks might also decrease net lactation weight loss by allowing sows to build up lost body reserves during the extra weeks of lactation, as is proposed for organic sows by Wientjes et al. (2011). From the third week of lactation onwards, milk yield is constant or even decreased and energy intake is high, since feed intake is at its maximum around week 3 to 4 of lactation. This can result in a less negative, or even positive, energy balance. Furthermore, piglets might also start eating creep feed during this period, which also reduces the suckling stimuli (Puppe and Tuchscherer, 2000). Since the weight of the suckling piglets also determines the amount of milk produced (King et al., 1997), replacing the 4 weeks old piglets with younger (lighter) piglets could decrease the energy expenditure for milk yield even more, and therefore increasing the positive effects on sow body development. However, due to hygiene and health risks, this might not be favourable.

7.3.3 Weaning to oestrus interval

The weaning to oestrus interval (WOI) is an important period in the reproductive cycle of sows. At weaning, FSH and LH release is increased in order to support follicle growth and development (reviewed by Quesnel, 2009). LH release, as well as follicle and oocyte development, during WOI are (in)directly influenced by several metabolic hormones and metabolites, such as insulin and IGF-1 (Van Den Brand et al., 2001a; Wientjes et al. 2012). Concentrations of these hormones are, in turn, influenced by the metabolic state of the sow (Table 7.1, Figure 3.2). Genetic selection for short WOI has led to sows that quickly return to oestrus after weaning and, as a result, usually are inseminated 4 to 5 days after lactation. Even though these sows exhibit oestrus and ovulate, pre- and post-weaning metabolic hormones and metabolites might have negatively affected follicle and oocyte quality (Zak et al., 1997b). Poor follicle or oocyte quality can lead to poorly developed embryos, increased embryonic mortality, and, eventually, to lower litter sizes or termination of pregnancy. Increasing the weaning to insemination interval by inseminating sows in the second rather than first oestrus after insemination, i.e. 'skip-a-heat', improves reproductive performance (Morrow et al., 1989; Clowes et al., 1994; Vesseur, 1997), possibly by reducing the metabolic influence on follicle and oocyte development. Similarly, sows showing a WOI of more than 19 to 21 days or that return to oestrus at 3 to 4 weeks after insemination, i.e. showing a natural 'skip-a-heat, give larger litter sizes than sows with a 4-5 day WOI (Vesseur, 1997; Chapter 2; Figure 7.1). Drawbacks of skip-a-heat, long weaning to insemination intervals and repeat breeders are the increase in non-productive days and the possible difficulty to

detect second oestrus, as has been reported for skip-a-heat sows by Clowes et al. (1994). Another option to allow sow recovery, without increasing the non-productive days by a full cycle, is extending the weaning to oestrus interval by feeding a synthetic progesterone analogue (reviewed by Van Leeuwen, 2011). The effects on reproductive performance, however, are variable and depend on parity, extent of lactation weight loss and the length of treatment (van Leeuwen, 2011). Furthermore, the use of hormones to 'repair' production related 'defects' might not be accepted by society.

7.4 Early gestation

During a reproductive cycle, gestation is the only period in which growth can be achieved (Dourmad et al., 1996). Growth during this period is especially important for first and second parity weaned sows, since they need to regain body reserves that were lost during lactation and they need to grow to reach their mature body size. Current gestation feeding schemes, however, often use (too) low feeding levels that cannot support both body reserve accretion and maternal growth. The low feeding levels are often based on the assumption that high feeding levels negatively influence embryonic survival, as has been reported for gilts (Jindal et al., 1996; De et al., 2009), but not in multiparous sows (Kirkwood et al., 1990; Varley and Prime, 1993; Virolainen et al., 2005b). In contrast, Sørensen and Thorup (2003) reported positive effects of an increased feeding level during early gestation on litter size in multiparous sows. Furthermore, an increased feeding level during early gestation can influence the secretion of uterine proteins and thereby improve embryonic development. Little information is available on the effects of a high feeding level during early second gestation on sow body development and reproductive performance in specifically (growing) second parity sows. We therefore performed two studies to investigate the effects of feeding level or feed composition on litter size and farrowing rate (Chapter 5) and embryonic development and endocrine profiles (Chapter 6).

7.4.1 Effects on reproduction

Results from Chapter 5 show that an increased (+30%, 3.25 kg/day vs. 2.5 kg/day) feed intake during early pregnancy improved subsequent litter size in second and third parity sows, without affecting piglet birth weight (Table 7.2). Results from Chapter 6, designed to find physiological explanations for results from Chapter 5, however, could not confirm the potential positive effects on litter size, estimated by the number of embryos at day 35 of gestation (Table 7.2).

Table 7.2 Combined results of Chapter 5 and 6 (for pregnant first parity sows only)

	Chapter 5		Chapter 6	
	Control	Plus Feed	Control	Plus Feed
Number of sows (n)	29	24	13	15
Reproduction				
Farrowing rate[1]/Pregnancy rate[2] (%)	83%	75%	87%	95%
Litter size[1]/ Vital embryos[2] (n)	12.0 ± 0.5^a	14.0 ± 0.5^b	15.9 ± 0.9	15.7 ± 0.7
Sow body development				
Average lactation weight loss (%)	9.3 ± 1.1	9.4 ± 1.1	14.7 ± 1.4	14.1 ± 1.4
<u>Gain first month of gestation[*]</u>				
Body weight (kg)	18.0 ± 1.1^{byz}	27.9 ± 1.2^{ax}	14.7 ± 1.3^{by}	20.0 ± 1.1^{az}
Loin muscle depth (mm)	3.5 ± 0.6	4.4 ± 0.6	2.8 ± 0.7	3.5 ± 0.6
Back fat depth (mm)	0.8 ± 0.4	1.6 ± 0.4	0.8 ± 0.5	1.9 ± 0.4

[1] Chapter 5, from first insemination after weaning; 2 Chapter 6, from first insemination after weaning,

[ab] indicate significant difference within Chapter; x,y,z indicate significant difference over Chapters
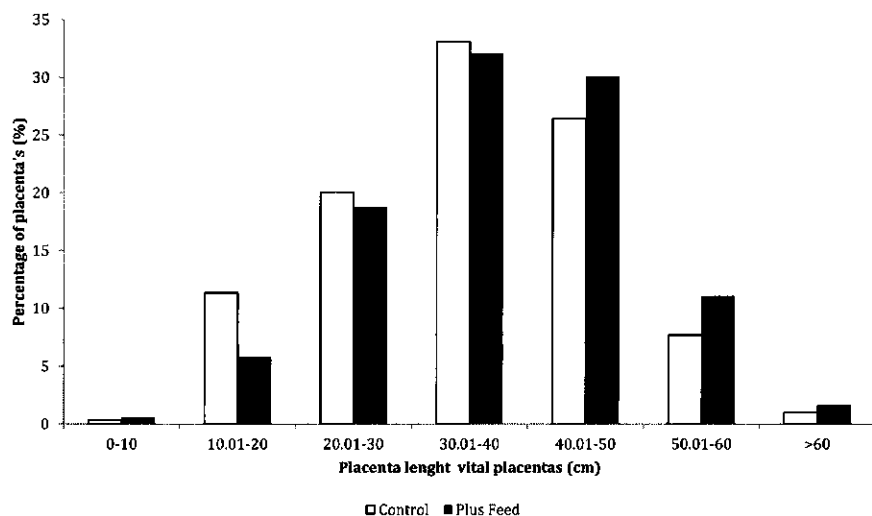
[*] for pregnant sows only

Figure 7.7 Distribution of placental length for placentas retrieved from sows on a control or high feeding level

Studying the number of embryos at day 35 as a measure for litter size at term can be difficult. Ovulation rate has increased in the past decade and, since uterine capacity is limited, uterine crowding plays an important role in embryonic and foetal losses from day 30 onwards (Vonnahme et al., 2002; Town et al., 2005). Therefore, other factors than embryonic survival up to day 35 might affect litter size at term. Vonnahme et al. (2002) report that the peak of prenatal losses probably lies around day 50 of gestation, and that these losses are mainly related to insufficient placental development. For example, Van Rens and Van der Lende (2000) report that day 35 embryos with placentas shorter than 40

cm or lighter than 40 grams will have an insufficient supply of nutrients and therefore will not reach their full growth potential, which might affect embryonic survival. Even though average placental length and weight were not different between sows on a high or control feeding level (Chapter 6), the distribution of placenta length in control sows seemed more skewed to shorter placentas than in sows on the high feeding level (Figure 7.7). This might indicate a beneficial effect of the high feeding level on placental length, which might affect foetal survival up to day 50 and eventually litter size at term. Thus, a higher feeding level might have positively influenced placental development (Chapter 6) and thereby embryonic survival up to term (Chapter 5).
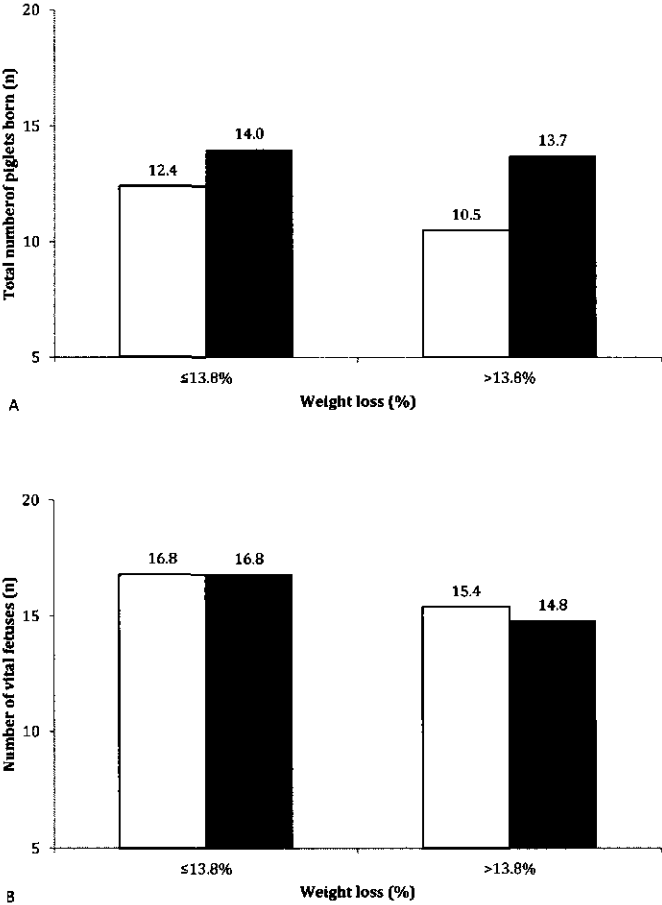

A

B

Figure 7.8 Effects of feeding level during early gestation on litter size (A, Chapter 5) and number of vital embryos (B, Chapter 6) for first parity sows with a low (≤13.8%) or high (>13.8%) weight loss. In order to compare chapter 5 and 6, the division of high and low weight loss is based on the median weight loss in Chapter 6. Open bars represent control feeding level (2.5 kg/d) solid bards represent the higher feeding level (3.25 kg/d). None of the differences were significant.

A difference between Chapter 5 and 6 was the weight loss of sows before the feeding treatment: first parity sows in Chapter 5 lost, on average, 5% less weight during lactation than first parity sows in Chapter 6 (9.5% vs. 14.5%, respectively). In Chapter 5, control sows with a higher than average weight loss (>9.5%) showed a numerically lower litter size than sows with a lower than average weight loss (≤9.5%, 12.4 ± 0.6 vs. 13.4 ± 0.5, respectively, P = 0.19) and the increased feeding level increased litter sizes in both high (+ 3 piglets) and low weight loss sows (+ 1 piglet). In Chapter 6 sows with a higher than average weight loss (>13.8%) tended to show a lower vital embryonic survival than sows with a low weight loss (≤13.8%; 14.9 ± 0.7 vs. 16.8 ±0.7, respectively, P = 0.07). However, in contrast to Chapter 5, feeding level did not improve embryonic survival in either high or low weight loss sows (Figure 7.8B). If similar weight loss groups are defined for Chapter 5 and 6, litter size in Chapter 5 sows (Figure 7.8A) is still numerically lower in high weight loss sows than in low weight loss sows. Further, using the 13.8% weight loss division, the higher feed intake still numerically improves litter size in both high and low weight loss sows. This indicates that other factors than weight loss explain the different effects of feeding level on litter size (Chapter 5) or number of vital embryos (Chapter 6).

High feeding levels have been reported to decrease systemic progesterone concentrations and thereby reducing embryonic survival in gilts (Jindal et al., 1996; De et al., 2008), whilst the effect in multiparous sows is less clear (Kirkwood et al. 1990, Varley and Prime 1993;(Virolainen et al., 2005b). The cause of the lower progesterone concentrations is an increased clearance in the liver , caused by a higher metabolism in sows on a high feeding level. To study if a higher feeding level also affected progesterone profiles in weaned primiparous sows, which could explain the litter size effect in Chapter 5, we measured progesterone concentrations during early pregnancy. As is described in Chapter 6, progesterone profiles were only marginally different between feeding levels, indicating that negative effects of a high feeding level on progesterone concentrations, as reported for gilts, are not present in weaned primiparous sows.

Systemic progesterone concentrations are a result of progesterone production on the ovaries and progesterone clearance in the liver. Progesterone produced by the CL on the ovaries, is transported to the uterus by a local counter current exchange system (Stefańczyk-Krzymowska et al., 1998) and uterine and endometrial development is therefore more related with ovarian progesterone production than with systemic progesterone concentration. Progesterone concentrations measured in the caudal vena cava, close to the ovaries (Virolainen et al., 2005a), therefore give a better indication of progesterone production than systemic concentrations. To get more insight the relations between systemic and local progesterone concentrations and their relation with feeding level, an additional six sows received a catheter in the caudal vena cava, as described by Benoit and Dailey (1991). These sows were treated the same as the other sows in the experiment described in Chapter 6.
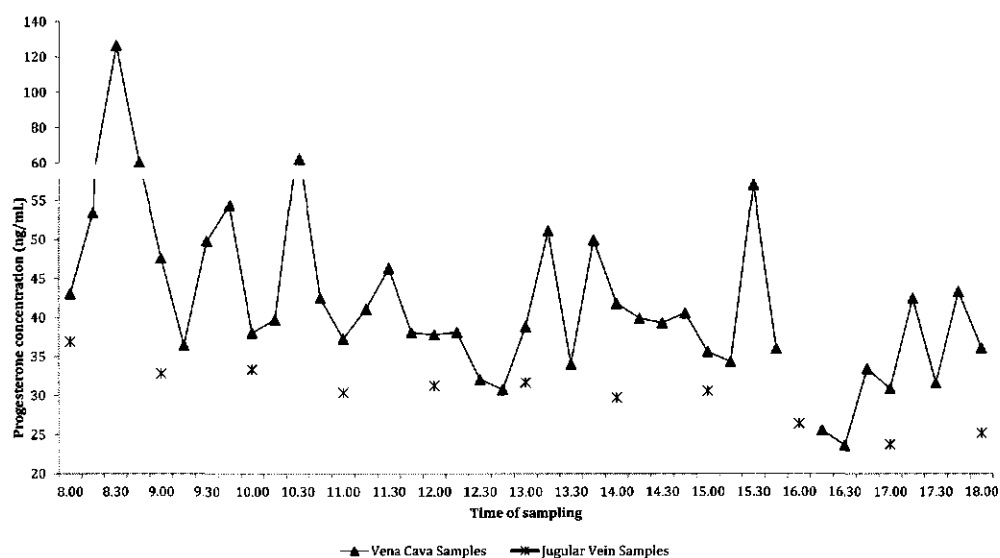
Figure 7.9 Progesterone profiles from vena cava (triangle) and jugular vein (cross) samples of a representative sow

As can be seen in Figure 7.9, progesterone measured in the vena cava on day 14 of gestation is released in a pulsatile manner as has been reported in gilts (Virolainen et al., 2005a) and miniature pigs (Parvizi et al., 1976). Furthermore, jugular vein samples show lower base levels of progesterone compared with vena cava samples. Preliminary analysis, however, do not show differences in vena cava progesterone concentration between sows on a control or high feeding level, indicating that a high feeding level may not have positively affect progesterone production on the ovaries in our experiment.

7.4.2 Effects on sow development

Results from both Chapter 5 and 6 show that an increased feeding level, i.e. 3.25 kg/d vs. 2.5 kg/d, increased sow body weight and numerically increased back fat and loin muscle depth during early gestation without negatively affecting reproductive performance (Table 7.2; Figure 7.10). However Chapter 5 and 6 show some differences when comparing absolute weight gain during early gestation (Figure 7.10A).

Weight gain during the first 4 weeks of gestation was the highest in the high feed sows from chapter 5 (27.9 ± 1.2 kg) and was the lowest for the control sows from chapter 6 (14.7 ± 1.3 kg). Interestingly enough, growth from the control sows from Chapter 5 and high feed sows from Chapter 6 was similar (18.0 ± 1.1 kg vs. 20.0 ± 1.1 kg, respectively). As a result, at day 35 of second gestation, weights of sows from Chapter 5 were similar to their weights after farrowing, whilst weights of Plus Feed sows from chapter 6 were in between and weight of Control sows from Chapter 6 were far lower than their weights
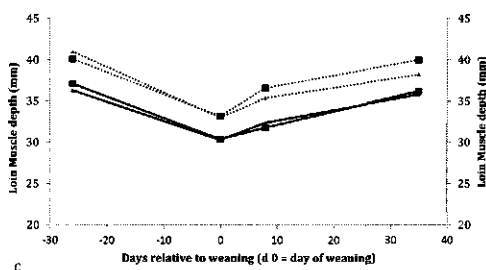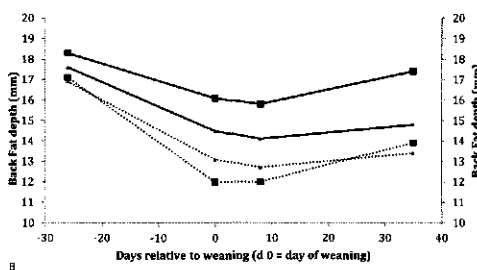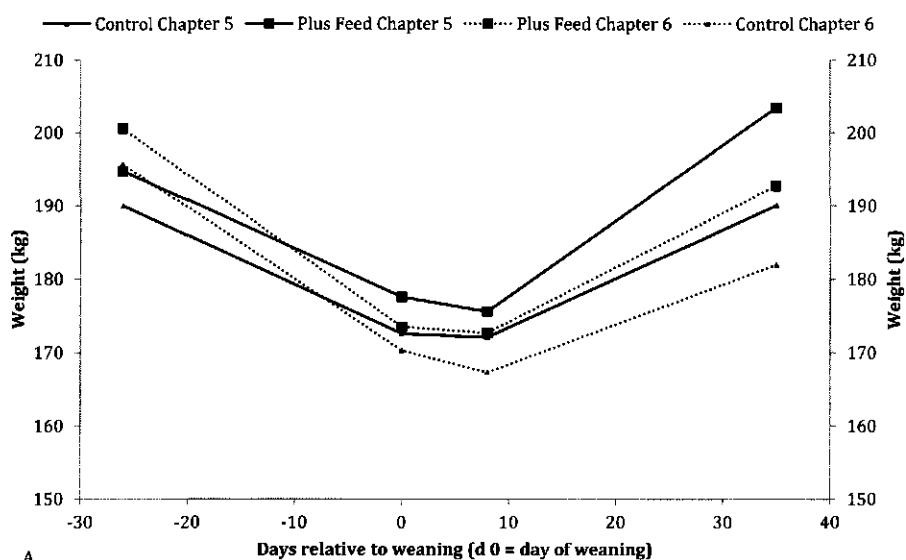
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Figure 7.10 Sow weight (A), Back fat depth (B) and Loin muscle depth (C) development from farrowing up to day 35 of second gestation for pregnant first parity Control (triangle)and Plus Feed (square) sows. Solid lines represents chapter 5 and dotted lines represent chapter 6.

after farrowing (Figure 7.10A). This indicates that the effects of an increased feeding level on sow body weight development is hard to predict. However, comparing two experiments done under different circumstances is difficult. Many factors that were different between experiments, such as climate and housing, sow treatment (blood sampling, etc.) and sow body composition (Figure 7.10B and 7.10C) could have affected the weight gain in response to feeding level. It might therefore also be difficult to predict the outcome of a high feeding level on sow bodyweight development and reproductive performance on individual farms.

In conclusion, an increased feeding level during early pregnancy does not negatively affect reproductive performance of second parity sows, and might even have a positive effect on litter size. Furthermore, it positively affects sow body weight development which is important for young sows.

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7.5 Practical Recommendations

When analysing reproductive performance of second parity sows, one should only use information on litter size from insemination(s) in the first cycle after weaning, i.e. non-repeat breeders, since litter sizes of repeat breeders are often high and can therefore mask low litter sizes in (second parity) sows.

On farm level, reduced reproductive performance in second parity compared with first parity can be used as an indicator of impaired reproductive performance in second parity sows. On sow level it cannot.

When quantifying effects of young sow productivity on later performance, the sum first and second parity litter size should be used rather than comparing second parity litter size with first parity litter size.

Gilt weight at first weaning should be higher than at first insemination, since sows that are heavier at first weaning than at first insemination show higher farrowing rates and litter sizes. This can be achieved by a higher growth rate during early gestation or reducing lactation weight loss.

Sow weight loss during lactation should be minimized to 10-14%. This can be achieved by altering lactation management in order to 1) increase lactation feed intake, 2) decrease suckling intensity during lactation or 3) increase lactation length, provided that sows have a high feed intake and piglets have access to creep feed.

An increased feed intake during early second gestation improves sow body weight development after first lactation, has no negative effects on reproductive physiology and performance and might even positively affect litter size in subsequent parity.

Related with the above, monitoring weight development of young sows is a valuable tool for sow management

7.6 Conclusions

Improved second parity reproductive performance results in a higher farm performance, both by improving reproductive performance and by increasing reproductive performance in later parities as well as sow longevity. This makes assessment of second parity reproductive performance of utmost importance.

Results from this thesis confirmed that repeat breeders in second and third parity have a higher subsequent litter size than non-repeat breeders. Therefore, when evaluating

reproductive performance of second parity sows, one should only use information from insemination(s) in the first cycle after weaning, i.e. non-repeat breeders.

Second parity sows may not only have low litter size, but may also have a higher number of repeat breeders. Therefore, when evaluating reproductive performance of second parity sows, the percentage of repeat breeders should be taken into account.
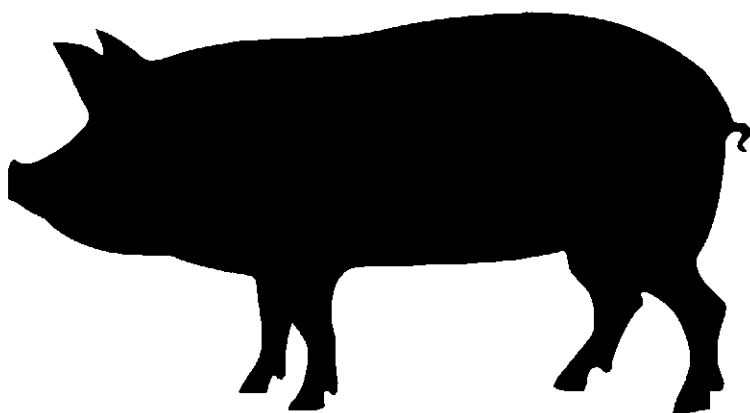
Results from this thesis show that weight loss during first lactation is, indeed, an important determinant for second parity reproductive performance (Chapter 2 and 3). Improving sow weight development up to first weaning can improve reproductive performance in second parity, as was shown in Chapter 2.

Results from Chapter 4 show that second parity litter size, as well as being a repeat breeder in second parity, are related with reproductive performance and culling in later parities. Furthermore, the sum of litter size in first and second parity seems to be an even better predictor for litter size in later parities than only second parity litter size.

As is shown in Chapter 5 and 6, an increased feeding level during early gestation will increase sow body development and might positively affect litter size in second parity.

Concluding, management practices in modern pig husbandry should focus on optimizing sow development up to first weaning, by optimizing sow body development in first gestation as well as minimising lactational weight loss during first lactation. Furthermore, increasing feed intake during early gestation will optimise sow body reserve recovery and might improve litter size in second parity.

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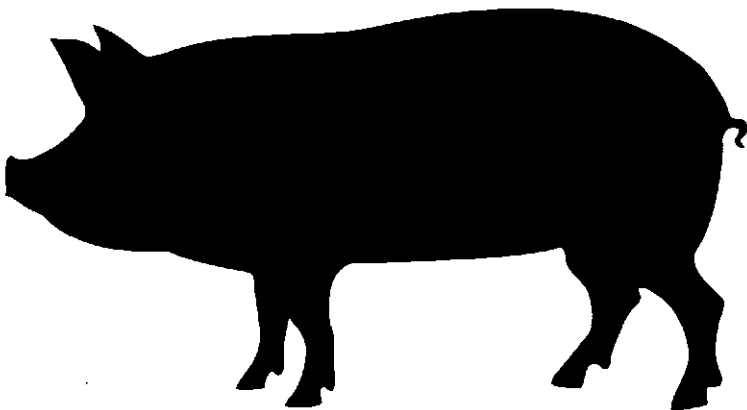
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Summary

Around 19% of the reproductive sows in a herd are second parity sows, i.e. sows of which their first ltiter is weaned. In general, reproductive performance. i.e. farrowing rate and litter size, increases with increasing parity, reaching the highest levels from parity 3 to 5(Koketsu et al., 1999; Hughes and Varley, 2003). Many second parity sows, however, show an equal or lower litter size than in their first parity. These lower litter sizes negatively influence farm productivity. Little is known about the relation between second parity reproductive performance and reproduction in later parities, however, poor subsequent reproductive performance may aggravate negative effects of farm productivity even more. The suboptimal reproductive performance in second parity has been related to (excessive) weight loss during first lactation. For potential post-lactation repair, it can be hypothesised that increasing the feeding level during early second gestation may improve sow body reserve recovery after lactation and might also improve subsequent reproductive performance. The aims of this thesis are to describe causes of variation in second parity litter size and farrowing rate, to describe relations between second parity reproductive performance and subsequent reproductive performance and to study if a different feed strategy during early gestation can improve reproductive performance and body weight recovery after lactation in second parity sows.

Causes of Variation

Suboptimal reproduction in second parity sows has been related to (excessive) weight loss during first lactation. Effects of weight loss during lactation on reproductive functioning, however, are often assessed at the embryonic stage and information on farrowing rate and litter size is scarce. More information on relations between sow weight development during first parity and farrowing rate and litter size in second parity may provide tools to optimize (feeding) management up to first weaning. The retrospective data-analysis in **Chapter 2** describes associations of body weight development during first parity with litter size and non-pregnancy in second parity, under practical circumstances. The study included data on sow body weight development and reproductive performance, routinely recorded on two experimental farms (farm A, N $\approx$ 271; farm B, N $\approx$ 203). The percentage non-pregnancy in second parity was 11% and 15% for farm A and B, respectively. For pregnant sows, second parity litter size was 11.6 ± 0.2 and 11.6 ± 0.6 piglets born total for farm A and B, respectively. An increased weight gain from first insemination to first weaning, i.e. in first parity, decreased the percentage non-pregnancy on both farms (odds ratio per 10 kg gain = 0.7 for farm A and 0.8 for farm B), and it increased litter size on farm A (β=0.42 piglet per 10 kg gain). This means that for every 10 kg heavier body weight at first weaning than at first insemination, the percentage non-pregnancy decreases and that litter size on farm A increases with 0.4 piglet. On farm A, non-pregnancy and litter size in second parity were mainly influenced by sow body weight development. On farm B other factors, such as total number of piglets born in first parity and sow line were related to non-pregnancy and litter size in second parity. The difference between both farms might

be related to gilt management, since gilts on farm A were lighter (124±0.5 vs. 145±0.8 kg) and younger (230±0.6 vs. 275±0.9 days) at first insemination compared with gilts on farm B. From this data-analysis it can be concluded that sow live weight development affects reproductive performance in second parity, especially on farm A where gilts are relatively light and young at first insemination. Furthermore, sows should be heavier at first weaning than at first insemination in order to improve farrowing rate in second parity.

From literature it is known that especially first parity sows are sensitive for lactation weight losses, as they do not have enough body reserves at first farrowing and have a limited feed intake capacity. Many studies have shown that feed or protein restriction during first lactation, as a model for weight loss, affects reproduction in second parity. In practise, however, sows are often fed (close to) ad libitum and variations in lactation weight loss are mainly due to variation in voluntary feed intake, milk production and maintenance costs. Effects of weight loss on reproductive functioning and metabolism might therefore be different during severe feed restriction than if feeding levels are close to ad libitum. Furthermore, most studies mainly focus on metabolic changes during lactation and the weaning to oestrus interval (WOI). However, metabolic differences present during lactation might still persist during (early) gestation and thereby influence embryonic survival. **Chapter 3** investigates associations of weight loss during lactation in mildly restricted first parity sows with reproductive performance on day 35 of second gestation and with metabolic profiles from the last 10 days of lactation until day 35 of second gestation. After weaning, 47 first parity sows were retrospectively assigned to a high (HWL, > 13.8%, n=24) or low (LWL, ≤ 13.8%, n=23) lactation weight loss group. Thirty-six animals received an indwelling jugular vein catheter to determine lactational and gestational profiles of Insulin-like Growth Factor-1 (IGF-1), Non-Esterified Fatty Acids (NEFA) and urea, lactational profiles of leptin and gestational profiles of progesterone. At day 35 after insemination sows were euthanized and their reproductive tract collected. Pregnancy rate was 75% (18/24) for HWL and 96% (22/23) for LWL sows. High weight loss sows had a lower embryonic survival (65.6 ± 3.4 vs. 77.4 ± 2.9%) than LWL sows, resulting in a lower number of vital embryos. During the last 10 days of lactation, HWL sows showed a tendency for higher NEFA concentrations compared with LWL sows, whilst IGF-1 and Urea concentrations were not significantly different between HWL and LWL sows. On day 4 after weaning urea concentration was higher for LWL than HWL sows. Progesterone peak values were reached 1.4 days later in HWL than in LWL sows, which might have negatively affected embryonic survival in HWL sows. Gestational concentrations of IGF-1, NEFA and urea were similar for HWL and LWL sows. No relation of the metabolic or hormonal variables, during lactation or gestation, with reproductive performance was found. This experiment shows that lactational weight loss in primiparous sows, when not imposed by severe feed or protein restriction, also negatively influences embryonic survival. These negative effects could not be attributed to differences in metabolic status of HWL and LWL sows in gestation, and were only mildly related with metabolic differences during lactation. The combined

results of Chapter 2 and 3 show that lactation weight loss is also an important determinant for second parity reproductive performance when weight loss is not induced by severe feed and protein restriction. However, the severity of the effects of lactation weight loss on reproductive performance in second parity might depend on other factors, for example body weight and composition at first farrowing.

Relations with subsequent reproduction

Around 50% of the second parity sows show a lower litter size in second compared with first parity. This reduced litter size decreases the reproductive efficiency of second parity sows but might also lead to early culling since reproductive failure is a common reason for culling in young sows. It is, however, not known if second parity reproductive performance is also related to reproductive performance in later parities. In **Chapter 4**, the relations between failure to farrow and litter size in second parity with reproductive performance in later parities are investigated. Firstly, 184,135 records from 46,571 sows were used to analyse effects of being a repeat breeder, i.e. return to oestrus after insemination, in second parity on subsequent farrowing rate, litter size and parity at culling. In total 15.7% of the sows inseminated after first weaning were a repeat breeder in second parity. Being a repeat breeder in second parity did not affect litter size in subsequent parities. However it was associated with a decreased farrowing rate in parity 3 (-4.1%) and 4 (-3.4%), but not in later parities. Repeat breeders in second parity were on average culled 2 parities earlier compared with non-repeat breeders (parity 5 vs. 7, respectively). Secondly, 161,521 records of 39,654 sows were used to analyse effects of litter size from first insemination after first weaning on subsequent litter size, farrowing rate and parity number at culling. Litter size in first parity was also included in the model as a class variable. Sows with a low litter size in second parity showed a lower litter size in parity 3 and up compared with sows with a medium or high litter size in second parity. Sows with a high litter size in second parity had 2% lower farrowing rate in parity 3, but not in later parities. Sows with a low litter size in second parity were culled 1 parity earlier compared with sows with a medium or high litter size in second parity. This data-analysis showed that a large part of the sows with poor reproductive performance in second parity can be expected to have a poor reproductive performance in subsequent parities. The effect of second parity litter size on subsequent litter size, however, also depends on first parity litter size. A higher first parity litter size decreased the effect of second parity litter size on subsequent litter size.

Gestation feeding strategy

Lactation has a large impact on sow body condition, especially for first parity sows that are physically immature and have relatively low body reserves at time of farrowing. An increased feeding level during early second gestation can help young sows to recover from lactation losses and might improve reproductive performance. However, in practise

feeding levels during early gestation are often low. The use of low feeding levels is based on studies in gilts, which report a reduced embryonic survival when using high feeding levels during early gestation. Little information is available on the effects of feeding level during early gestation on reproductive performance in second parity sows. In **Chapter 5**, we therefore investigated if an increased feed or protein level during the first 4 weeks of second or third gestation improves recovery from lactation losses and litter size and farrowing rate in subsequent parity. From days 3 to 32 after first insemination after weaning, sows were fed either 2.5 kg/day of a standard gestation diet (Control, n = 49), 3.25 kg/day (+30%) of a standard gestation diet (Plus Feed, n = 47) or 2.5 kg/day of a gestation diet with 30% greater ileal digestible amino acids (Plus Protein, n = 49). Sows in the Plus Feed group gained 10 kg more body weight during the experimental period compared with those in the Control and Plus Protein group. Litter size from first insemination was larger for sows in the Plus Feed group (15.2 ± 0.5 total born) compared with those in the Control and Plus Protein groups (13.2 ± 0.4 and 13.6 ± 0.4 total born, respectively). Despite the larger litter size in Plus Feed sows, piglet birth weight was not different among treatments. Farrowing rate, however, was numerically lower for sows in the plus feed group compared with those in the control and plus protein groups (76.6% vs. 89.8 and 89.8%, respectively). Results from this experiment showed that an increased feed intake (+30%) during the first month of gestation improved sow body weight recovery and increased litter size in subsequent parity. Feeding a 30% higher level of ileal digestible amino acids during the same period did not improve sow recovery or reproductive performance in subsequent parity.

Based on the results in Chapter 5, hormonal and metabolic alterations related to feeding level and their relation with reproductive performance during the first 35 days of second gestation were investigated in **Chapter 6**. Sows received either a control (2.5 kg/day) or high (3.25 kg/day) feeding level from day 3 to 35 after first insemination after weaning. Frequent blood samples were taken for progesterone, LH, glucose, insulin, insulin-like-growth-factor-1 (IGF-1), non-esterified-fatty-acids (NEFA) and urea analysis. At day 35 after insemination sows were euthanized and their reproductive tract collected to assess ovarian, embryonic and placental characteristics. In this experiment Plus Feed sows gained 5.4 kg more weight and 0.9 mm more back fat and tended to be heavier at slaughter compared with Control sows. Treatment did not affect vital embryonic survival, which was 72.1 ± 3.9% for Control and 73.4 ± 3.2% for Plus Feed sows. No effect of treatment on any of the ovarian, embryonic, placental, progesterone or LH characteristics were found. Insulin peaked later (48 vs. 24 min post feeding) and at a higher concentration in Plus Feed than in Control sows. NEFA concentrations were lower for Plus Feed vs. Control sows (149 ± 9 vs. 182 ± 12 μm/l, respectively) and urea concentration tended to be higher in Plus Feed than in Control sows (4.3 ± 0.1 vs. 3.9 ± 0.1 ng/mL, respectively). None of the metabolic variables were related to reproductive measures. In conclusion, feeding 30% more feed from Day 3 till d 35 of second gestation increased weight gain and resulted in lower NEFA concentrations, but did not affect progesterone, LH or IGF-1 and embryonic and placental

characteristics. The combined results of chapter 5 and 6 show that an increased feeding level during early gestation can improve sow development without affecting plasma progesterone concentrations and embryonic survival and might be beneficial for litter size in subsequent parity. However the physiological mechanisms behind the improved litter sizes in Chapter 5 remain unclear.
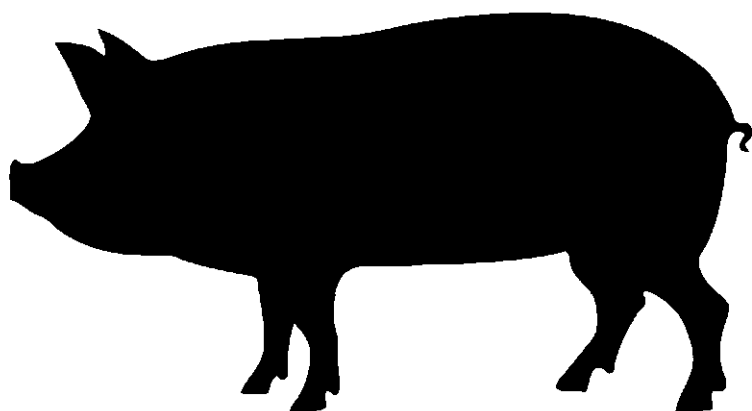
Conclusions

An improved reproductive performance of second parity sows results in a higher farm performance, both by increasing second parity reproductive performance and by increasing reproduction in later parities as well as sow longevity.

When evaluating second parity reproductive performance, only information from first insemination in the first cycle after weaning should be used, since repeat breeders often show higher litter sizes and inclusion of repeat breeder litter size might therefore mask low productivity of (second) parity sows. Since second parity sows might not only show reduced litter sizes, but also an increased percentage of repeat breeders, the percentage of repeat breeders should also be taken into account when evaluation second parity reproductive performance.

Lactation weight loss is an important determinant for reproductive performance in second parity sows. Sow development up to first farrowing, however, can influence the effects of lactation weight loss on reproductive performance. Sow farmers should therefore pay special attention to their gilt management strategies up to first insemination, but certainly also during first gestation. Even though this thesis did not specifically investigate maximum weight losses in relation to reproductive performance, it can be concluded that maximum weight loss during first lactation should be between 10-14% in order to achieve good reproduction results in second parity.

A higher feeding level during early second gestation positively affects sow body reserve recovery without negatively affecting progesterone concentrations or embryonic survival. Furthermore, an increased feeding level during early second gestation can improve second parity litter size, however, the physiological mechanisms through which feeding level affects reproductive performance remain unclear.

Samenvatting

Ongeveer 19% van de zeugen op een bedrijf zijn tweede worps zeugen, i.e. zeugen waarvan de eerste worp is gespeend. In het algemeen stijgen het afbigpercentage en de toomgrootte naarmate het cyclusnummer toeneemt en laten cyclus 3-5 zeugen de hoogste resultaten zien (Koketsu et al., 1999; Hughes and Varley, 2003). Helaas hebben veel zeugen een vergelijkbare of lagere toomgrootte in de tweede worp dan in de eerste worp, de zogenaamde 'tweede worps dip'. Deze tweede worps dip heeft een negatief effect op de bedrijfsproductiviteit. Er is weinig bekend over de relatie tussen de reproductie in de tweede worp en de reproductie in de volgende worpen. Als er een relatie is wordt de reproductie in de tweede worp mogelijk nog belangrijker voor de bedrijfsresultaten. De verminderde reproductie resultaten in de tweede worp zijn vooral gerelateerd aan (grote) gewichtsverliezen tijdens de eerste lactatie. Een verhoogd voerniveau in de vroege dracht kan een mogelijke oplossing zijn om de zeug helpen te herstellen van de lactatie en de negatieve effecten van lactatie gewichtsverlies op reproductie te verminderen of op te heffen. Het doel van dit proefschrift is om de oorzaken van de variatie in de toomgrootte en het afbigpercentage in tweede worp te beschrijven, relaties tussen de toomgrootte en het afbigpercentage in de tweede worp en de latere reproductie te beschrijven en om te onderzoeken of een aangepaste voerstrategie in de vroege dracht de reproductieresultaten in de tweede worp én het lichaamsherstel van de zeug na lactatie kan verbeteren.

Oorzaken van variatie

Suboptimale reproductie in de tweede worp wordt vooral veroorzaakt door (grote) gewichtsverliezen tijdens de eerste lactatie. Hierbij moet opgemerkt worden dat de gevolgen van gewichtsverlies op de reproductie meestal zijn onderzocht op embryonaal niveau en er weinig informatie is over de effecten van gewichtsverlies op afbigpercentage en toomgrootte. Meer informatie over de relatie tussen de gewichtsontwikkeling, in de periode tussen de eerste levensinseminatie en eerste keer spenen, en reproductie in de tweede worp kan een waardevolle tool zijn om het (voer) management van gelten tijdens de periode van eerste levensinseminatie tot en met de eerste keer spenen te optimaliseren. De retrospectieve data-analyse van **Hoofdstuk 2** beschrijft, onder praktijk omstandigheden, de relaties tussen gewichtsontwikkeling tijdens de eerste cyclus en de toomgrootte en het risico op niet drachtig worden in de tweede worp. Voor deze analyse zijn routinematig geregistreerde gewichts- en reproductiegegevens van twee proefbedrijven (bedrijf A, n ≈ 271; bedrijf B n = ≈ 203) gebruikt. Het percentage niet-drachtige tweede worps zeugen was 11% voor bedrijf A en 15% voor bedrijf B. De toomgrootte vanuit eerste inseminatie van tweede worps zeugen was 11.6 ± 0.2 (bedrijf A) en 11.6 ± 0.6 (bedrijf B). Op beide bedrijven nam het percentage niet-drachtige zeugen af naarmate de gewichtstoename van eerste levensinseminatie tot en met eerste keer spenen groter was (odds ratio per 10 kilo extra gewichtstoename 0.7 voor bedrijf A en 0.8 voor bedrijf B). Op bedrijf A nam ook de toomgrootte in de tweede worp met 0.4 big toe als de gewichtstoename tussen eerste levensinseminatie en eerste keer spenen met 10 kilo toenam. Verder bleek uit de

resultaten dat op bedrijf A het percentage niet-drachtige zeugen en de toomgrootte in de tweede worp vooral gerelateerd waren aan de lichaamsontwikkeling van de zeugen. Op bedrijf B waren het met name andere factoren die het percentage niet-drachtige zeugen en de toomgrootte beïnvloedden. Dit verschil zou gerelateerd kunnen zijn aan het feit dat de gelten op bedrijf A lichter (124 ± 0.5 vs. 145 ±0.8 kg) en jonger (230 ± 0.6 vs. 275 ± 0.9 dagen) waren ten tijde van de eerste levensinseminatie dan gelten op bedrijf B. Uit deze data-analyse kan geconcludeerd worden dat de gewichtsontwikkeling van zeugen in de eerste cyclus gerelateerd is aan de reproductieresultaten in de tweede worp, vooral op bedrijf A waar de gelten relatief licht en jong zijn ten tijde van de eerste levensinseminatie. Om het afbigpercentage in de tweede worp te verbeteren moeten zeugen daarom zwaarder zijn bij de eerste keer spenen dan bij de eerste levensinseminatie.

Uit de literatuur is het bekend dat vooral tweede worps zeugen gevoelig zijn voor de negatieve effecten van gewichtsverlies tijdens de lactatie. Deze jonge zeugen hebben namelijk nog niet voldoende lichaamsreserves ten tijde van de eerste keer afbiggen en hebben een relatief lage voeropname capaciteit. Veel studies hebben aangetoond dat voer- of eiwitbeperking tijdens de eerste lactatie, gebruikt als model voor gewichtsverlies, de reproductie in de volgende worp negatief beïnvloed. In in de praktijk worden zeugen meestal (bijna) ad libitum gevoerd en wordt de variatie in gewichtsverlies tijdens de lactatie vooral veroorzaakt door de variatie in voeropname, melk productie en onderhoudsbehoefte. Hierdoor zouden de effecten van gewichtsverlies op reproductie en het metabolisme in de experimenten anders kunnen zijn dan in de praktijk. Daarbij focussen de meeste experimenten alleen op metabole veranderingen tijdens de lactatie en het interval-spenen-dekken (ISD), terwijl de metabole veranderingen tijdens de lactatie mogelijk ook in de vroege dracht kunnen blijven bestaan. Dit zou de embryonale overleving tijdens de dracht ook nog kunnen beïnvloeden. **Hoofdstuk 3** beschrijft de relaties van gewichtsverlies tijdens de lactatie met embryonale overleving op dag 35 van de dracht en de metabole profielen van de laatste 10 dagen van de lactatie tot aan dag 35 van de dracht, in zeugen met een milde voerbeperking. Na het spenen werden 47 eerste worps zeugen in een hoog (HG, >13.8%, n = 24) of laag (LG, ≤13.8%, n = 23) gewichtsverlies groep ingedeeld. Zesendertig zeugen kregen een canule om insulin-like-growthfactor-1 (IGF-1), non-esterified fatty acids (NEFA) en ureum profielen te bepalen tijdens de lactatie en de dracht en progesteron profielen tijdens de dracht. Op dag 35 werden de zeugen geeuthanaseerd en hun reproductiestelsel geanalyseerd. Het drachtpercentage was 75% (18/24) voor de HG en 96% (22/23) voor de LG zeugen. HG zeugen hadden een lagere embryonale overleving op dag 35 (65.6 ± 3.4 vs. 77.4 ± 2.9%) dan LG zeugen, wat resulteerde in een lager aantal vitale embryo's. Tijdens de laatste 10 dagen van de dracht neigden de NEFA concentraties van HG zeugen hoger te zijn dan de NEFA concentraties van de LG zeugen, terwijl de IGF-1 en ureum concentraties niet significant verschillend waren tussen HG en LG zeugen. Op dag 4 na het spenen waren de ureum concentraties significant hoger in LG dan in HG zeugen. In de HG zeugen bereikte progesteron zijn maximale niveau 1.4 dagen later dan in

de LG zeugen, wat de embryonale overleving mogelijk negatief beïnvloed kan hebben. De IGF-1, NEFA en ureum concentraties tijdens de dracht waren niet significant verschillend tussen de HG en LG zeugen. Er zijn ook geen relaties tussen de metabole of hormonale kenmerken tijdens de lactatie of dracht, en de reproductiekenmerken gevonden. Uit dit experiment kan geconcludeerd worden dat gewichtsverlies tijdens de lactatie, ook als het niet geïnduceerd is door voer- of eiwitbeperking, de embryonale overleving op dag 35 van de dracht beïnvloed. Deze negatieve beïnvloeding kan niet worden toegewezen aan verschillen in de gemeten metabole kenmerken tijdens de dracht, en mogelijk maar voor een klein deel aan verschillen in de metabole kenmerken tijdens de lactatie. Zowel de resultaten uit hoofdstuk 2 als hoofdstuk 3 tonen aan dat gewichtsverlies tijdens de eerste lactatie een groot effect heeft op de reproductie in de tweede worp, ook als gewichtsverlies niet veroorzaakt wordt door voer- of eiwitbeperking. De mate waarin het gewichtsverlies de reproductie beïnvloedt, hangt af van factoren zoals lichaamsgewicht en –samenstelling bij het werpen.

Relaties met reproductie in de volgende worpen.

Ongeveer 50% van de zeugen heeft een kleinere toom in de tweede worp dan in de eerste worp. Deze verminderde toomgrootte verlaagt de reproductie efficiëntie van tweede worps zeugen, maar kan ook de leeftijd bij ruimen vervroegen, omdat slechte reproductie een veel voorkomende reden is om jonge zeugen te ruimen. Er is weinig informatie over de relatie tussen reproductieresultaten, i.e. afbigpercentage en toomgrootte, in de tweede worp en de reproductieresultaten in de volgende pariteiten. In **Hoofdstuk 4** worden de relaties tussen het niet-drachtig worden en de toomgrootte in de tweede worp en de reproductieresultaten in de latere pariteiten beschreven. Al eerste zijn 184,135 waarnemingen van 46.571 zeugen geanalyseerd om de relatie tussen terugkomen in de tweede worp en het afbigpercentage en de toomgrootte in de volgende worpen en de pariteit bij afvoer te bepalen. In totaal waren er 15.7% terugkomers vanuit de eerste inseminatie in de tweede worp. Het terugkomen in de tweede worp had geen effect op de toomgrootte in de volgende pariteiten. Zeugen die in de tweede worp teruggekomen waren hadden een lager afbigpercentage als derde (-4.1%) en vierde (-3.4%) worps zeug. Het afbigpercentage in de worpen daarna was niet meer beïnvloed. Zeugen die zijn teruggekomen in de tweede worp werden, gemiddeld, 2 worpen eerder afgevoerd dan zeugen die niet terugkwamen (respectievelijk worp 5 vs. 7). Als tweede werden 161.521 waarnemingen van 36.654 zeugen gebruikt om de relaties tussen toomgrootte vanuit de eerste inseminatie in de tweede worp en het afbigpercentage en de toomgrootte in de volgende worpen en de pariteit bij afvoer te analyseren. Als extra is ook de toomgrootte van de eerste worp is in de analyse meegenomen. In vergelijking met zeugen met een gemiddelde of hoge toomgrootte in de tweede worp hadden zeugen met een lage toomgrootte in de tweede worp ook een lagere toomgrootte in pariteit 3 en ouder en werden ze 1 pariteit eerder afgevoerd. Zeugen met een hoge tweede worp hadden een 2% lager afbigpercentage in de derde worp, maar niet in de oudere pariteiten. Uit deze

data-analyse kan geconcludeerd worden dat een groot deel van de zeugen met verminderde reproductieresultaten in de tweede worp ook verminderde reproductieresultaten in de volgende pariteiten zullen hebben. Hierbij moet opgemerkt worden dat het effect van de toomgrootte in de tweede worp op de toomgrootte in de volgende pariteiten beïnvloed wordt door de toomgrootte in de eerste worp.

Voerstrategie tijdens de vroege dracht

De lactatie heeft een grote invloed op de lichaamsconditie van zeugen. Dit geldt in het bijzonder voor de eerste worps zeugen die lichamelijk nog onvolwassen zijn en relatief weinig lichaamsreserves hebben bij de eerste keer werpen. Een verhoogd voerniveau tijdens de vroege tweede dracht zou het lichaamsherstel mogelijk kunnen stimuleren en de reproductieresultaten in de tweede worp verbeteren. In de praktijk zijn de voerniveaus tijdens de vroege dracht over het algemeen laag. Deze lage(re) voerniveau zijn gebaseerd op experimenten met gelten, waarin de embryonale overleving verminderd als gelten een verhoogd voerniveau krijgen. Er is weinig informatie beschikbaar over de effecten van hogere voerniveaus tijdens de vroege dracht op de reproductieresultaten van tweede worps zeugen. In **Hoofdstuk 5** is daarom onderzocht of een verhoogd voer- of eiwitniveau tijdens de eerste vier weken van de tweede of derde dracht het lichaamsherstel na lactatie kan bevorderen en afbigpercentage en de toomgrootte in de tweede en derde worp kan verbeteren. Van dag 2 tot 32 na inseminatie kregen de zeugen 2.5 kilo/dag van een standaard drachtvoer (Controle, n = 49) of 3.25 kilo/dag (+30%) van het standaard drachtvoer (Plus Voer, n = 47) of 2.5 kilo/dag van een drachtvoer met 30% meer darm verteerbare aminozuren (Plus Eiwit, n = 49). De gewichtstoename tijdens de proefperiode was 10 kilo hoger voor de Plus Voer zeugen dan voor de Controle en Plus Eiwit zeugen. De toomgrootte vanuit eerste inseminatie was ook hoger voor de Plus Voer zeugen (15.2 ± 0.5 totaal geboren) dan voor de Controle en Plus Eiwit zeugen (respectievelijk 13.2 ± 0.4 en 13.6 ± 0.4 totaal geboren). Ondanks de grotere tomen, was het geboortegewicht van de biggen uit de Plus Voer zeugen niet lager dan de geboortegewichten van de biggen uit de Controle en Plus Eiwit zeugen. Het afbigpercentage tendeerde lager te zijn in de Plus Voer zeugen dan in de Controle en Plus Eiwit zeugen (76.6% vs. 89.8 en 89.8%, respectievelijk), maar dit verschil was niet significant. Uit dit experiment kan geconcludeerd worden dat een verhoogd (+30%) voerniveau, tijdens de eerste maand van de tweede of derde dracht het lichaamsherstel van zeugen bevorderd en de toomgrootte in de volgende worp verbeterd. Een verhoogd percentage darm verteerbare aminozuren had geen positieve effecten op lichaamsherstel of toomgrootte.

In **Hoofdstuk 6** zijn, gebaseerd op de resultaten van hoofdstuk 5, de mogelijke door het verhoogde voerniveau geïnduceerde metabole en hormonale veranderingen en hun relatie met de reproductieresultaten in de eerste 35 dagen van de tweede dracht onderzocht. Van dag 3 tot 35 na de eerste inseminatie na het spenen kregen de zeugen 2.5 kilo/dag

(Controle) of 3.25 kilo/dag (Plus Voer) van een standaard drachtvoer. Er werd frequent bloed afgenomen wat werd geanalyseerd op progesteron, luteïniserend hormoon (LH), IGF-1, NEFA en Ureum. Op dag 35 van de dracht werden de zeugen geëuthanaseerd en de eierstokken, baarmoeder, embryo' s en placenta's beoordeeld. In dit experiment hadden de Plus Voer zeugen tijdens de proefbehandeling een 5.4 kilo hogere gewichtstoename en 0.9 hogere spekdikte toename van de Controle zeugen, wat resulteerde in een tendens voor een hoger gewicht aan het einde van de proefbehandeling. De proefbehandeling had geen effect op de embryonale overleving. Deze was $72.14 \pm 3.9\%$ voor de Controle zeugen en $73.4 \pm 3.2\%$ voor de Plus Voer zeugen. Er werden ook geen verschillen gevonden tussen de proefbehandelingen ten aanzien van de kenmerken van de eierstokken, baarmoeder, embryo's, placenta's, progesteron of LH. De insuline niveaus piekten later (48 vs. 24 minuten na het voeren) en met een hogere concentratie in de Plus Voer dan in de Controle zeugen. NEFA concentraties waren lager in de Plus Voer dan in de Controle zeugen ($149 \pm$ 9 vs. 182 ± 12 µm/l, respectievelijk) en ureum neigde hoger te zijn inde Plus Voer dan in de Controle zeugen (4.3 ± 0.1 vs. 3.9 ± 0.1 ng/ml, respectievelijk). Geen van de metabole parameters waren gerelateerd aan de reproductiekenmerken. Concluderend kan worden dat het voeren van 30% meer voer van dag 3 tot 35 in de tweede dracht resulteerde in een hogere gewichtstoename en lagere NEFA concentraties en dat de progesteron, LH, IGF-1 en de embryonale en placenta kenmerken niet waren beïnvloed. De resultaten van hoofdstuk 5 en 6 laten zien dat een verhoogd voerniveau tijdens de vroege dracht het lichaamsherstel van de zeug bevorderd zonder effect te hebben op plasma progesteron concentraties en embryonale overleving, verder kan een verhoogd voerniveau de toomgrootte in de tweede worp positief beïnvloeden. Het fysiologische mechanisme voor de positieve resultaten uit hoofdstuk 5 blijft helaas onbekend.
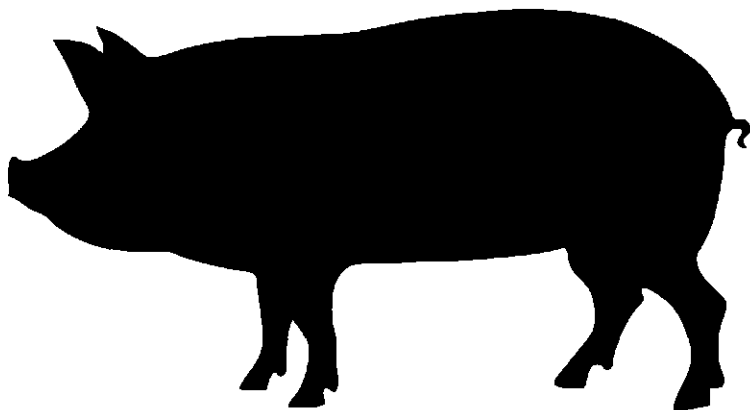
Conclusies

Een verbeterd afbigpercentage of toomgrootte in de tweede worp resulteert in verbeterde reproductieresultaten op bedrijven, zowel door het productieniveau van tweede worps zeugen te verbeteren als door het productie niveau van oudere pariteiten te verbeteren.

Bij het analyseren van de reproductieresultaten van tweede worps zeugen, moeten alleen de gegevens uit de inseminaties in de eerste cyclus na het spenen, d.w.z. zonder terugkomers, gebruikt worden. Omdat de toomgrootte van terugkomers vaak hoger is dan de toomgrootte van niet-terugkomers kan het gebruik van zowel terugkomers als niet-terugkomers de werkelijke toomgrootte in de tweede worp maskeren. Omdat de tweede worps dip niet alleen bestaat uit een verminderde toomgrootte, maar ook kan bestaan uit een verhoogd percentage terugkomers, moet het percentage terugkomers in de tweede worp ook meegenomen worden in de beoordeling van de reproductieresultaten in de tweede worp.

Gewichtsverlies tijdens de eerste lactatie heeft een grote invloed op de reproductieresultaten van tweede worps zeugen, maar de groei en ontwikkeling van gelten tot aan de eerste keer werpen kan de effecten van gewichtsverlies op reproductie beïnvloeden. Zeugenhouders moeten daarom extra aandacht geven aan de ontwikkeling en het management van gelten tot aan eerste inseminatie, maar zeker ook tijdens de eerste dracht. Ondanks dat dit proefschrift niet specifiek heeft gekeken naar de maximale gewichtsverliezen tijdens de eerste lactatie in relatie tot reproductie, kan er geconcludeerd worden dat zeugen tijdens de eerste lactatie maximaal 10 tot 12% gewicht mogen verliezen zonder dat de reproductie in de tweede worp negatief beïnvloed wordt.

Een verhoogd voerniveau tijdens de vroege tweede dracht heeft een positief effect op het lichaamsherstel van tweede worps zeug na lactatie, zonder de progesteronniveaus of embryonale overleving negatief te beïnvloeden. Een verhoogd voerniveau tijdens de vroege tweede dracht kan zelfs een positief effect hebben op de toomgrootte in de volgende worp, maar het fysiologische mechanisme achter dit positieve effect niet verklaard worden met behulp van dit proefschrift.

About the Author

Lia Liesanna Hoving was born on the second of July 1980, in Leeuwarden, The Netherlands. In 1998 she graduated from high school at C.S.G. Liudger in Drachten. After her exam she decided to broaden her view of the world and attended Cedercrest High School in Duvall (USA). In 1999 Lia started her study 'Animal Sciences' at Wageningen University, which she temporarily put on hold to work as a horsetrainer at DG Bar Ranch in Handford (USA). After resuming her study she chose the specialization 'Animal Health, Welfare and Management'. For her major thesis at the Adaptation Physiology Group she studied if saliva and vaginal and cervical mucus could predict estrus in dairy cattle. During her thesis she also worked as a technical assistant at the Adaptation Physiology Group and participated in several swine and dairy cattle experiments. She conducted her minor thesis at the Quantitative Veterinary Epidemiology Group of Wageningen University in combination with the University of Warwick (UK). During this thesis she studied the prevalence of bovine viral diarrhea (BVD) in UK cattle herds. For her externship she studied the effects of growth rate on gilt response to boar exposure and puberty attainment at the Pig and Poultry Production Institute in Roseworthy (Australia). After her graduation in November 2005, Lia started working as a reproduction consultant at 'Varkens KI Limburg, which later merged with 'Varkens KI Noord-Brabant' and 'Varkens-Activiteiten-Centrum' to become 'Varkens KI Nederland'. After 6 months she combined her work as reproduction consultant with the PhD research of which this thesis is the result.

List of Publications

Scientific Refereed Journals
- Hoving, L.L., Soede, N.M., Graat, E.A.M., Feitsma, H. & Kemp, B. (2010). Effect of live weight development and reproduction in first parity on reproductive performance of second parity sows. *Animal Reproduction Science, 122(1-2), 82-89.*
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- Hoving, L.L., Soede, N.M., Peet-Schwering, C.M.C. van der, Graat, E.A.M., Feitsma, H. & Kemp, B. (2011). An increased feed intake during early pregnancy improves sow body weight recovery and increases litter size in young sows. *Journal of Animal Science, 89(11), 3542-3550.*
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- Kemp, B., Wientjes, J.G.M., Leeuwen, J.J.J. van, Hoving, L.L. & Soede, N.M. (2011). Key

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- Kemp, B., Wientjes, J.G.M., Leeuwen, J.J.J. van, Hoving, L.L. & Soede, N.M. (2011). Nutrition and management during lactation: effects on future parity productivity. In *Proceedings of the 2011 Manitoba Swine Seminar, 2-3 February 2011, Manitoba, Canada* (pp. 85-97). Manitoba.
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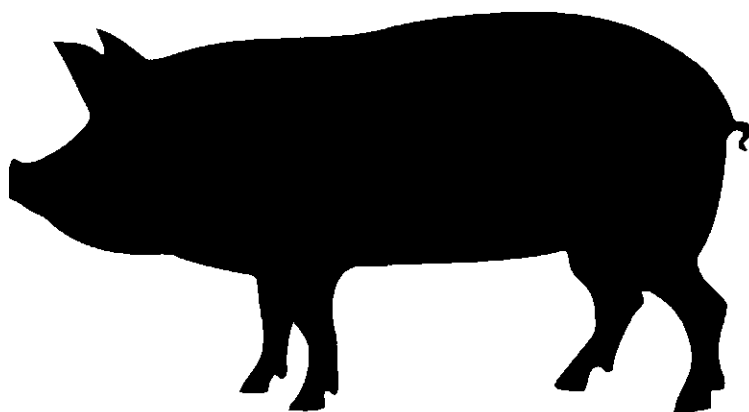- Hoving, L.L., Peet-Schwering, C.M.C. van der, Kemp, B. & Soede, N.M. (2008). Groei belangrijk voor tweedeworps zeug. V-focus, 5(april (2)), 44-45.
- Hoving, L.L., Peet-Schwering, C.M.C. van der, Dirx-Kuijken, N.C.P.M.M. & Soede, N.M. (2010). *Voeding tijdens de vroege dracht: effecten op reproductie en lichaamsontwikkeling van jonge zeugen = Feeding during early gestation: effects on reproduction and body development in young sows.* (Rapport / Wageningen UR Livestock Research 378). Lelystad: Wageningen UR Livestock Research.

WIAS Training and Supervision Plan

The Basic package (3.0 ECTS)	Year
WIAS Introduction Course	2007
WIAS course on philisophy and ethics	2009
International Conferences (5.1 ECTS)	
Paradigms in Pig Science	2007
European Society of Domestic Animal Reproduction (ESDAR), Celle, Germany	2007
European Society of Domestic Animal Reproduction, Utrecht, The Netherlands	2008
European Society of Domestic Animal Reproduction, Ghent, Belgium	2009
International Conference on Pig Reproduction (ICPR), Banff, Canada	2009
International Conference of Production Diseases (ICPD), Ghent, Belgium	2010

Seminars and workshops (1.8 ECTS)	Year
WIAS Science Day	2007
European AI Vets, Celle, Germany	2007
WIAS Science Day	2008
European AI Vets, Utrecht, The Netherlands	2008
WIAS Science Day	2009
WIAS Science Day	2010
Presentations (5 ECTS)	
ESDAR, Celle, Germany, Poster presentation	2007
ESDAR. Utrecht, The Netherlands, Oral presentation	2008
ICPR, Banff, Canada, Two poster presentations	2009
ICPD, Ghent, Belgium, Oral Presentation	2010
In Depth Studies (7.2 ECTS)	
PHLO Course 'Vruchtbaarheid en Voortplanting van het Varken', Wageningen Business School, Wageningen	2006
PHLO Course 'Varkensvoeding in de praktijk', Wageningen Business School, Wageningen	2006
Design of Animal Experiments, WIAS, Wageningen	2007
Statistics for the life sciences, WIAS, Wageningen	2007
Epigenesis and Epigenetics, VLAG, Wageningen	2008
Domestic Animal Reproduction: The Ovary. NOVA course, Helsinki, Finland	2010
Professional Skills Support Courses (5.2 ECTS)	
Techniques for writing and presenting a scientific paper, WIAS, Wageningen	2007
Supervising MSc thesis work,	2007
PhD competence assesment, WIAS, Wageningen	2007
Communication with the media and general Public,	2010
'Congruentiemanager', Delphi Group, Netherlands	2009-2010
Research skills training (4 ECTS)	
Preparing own PhD research proposal	2006-2007
Didactic Skills Training (20.4 ECTS)	
Lecture "	2009 and 2010
Lecture in Reproduction and Fertility course	2009 and 2010
Supervision yearly practical course 'Reproduction and Fertility'	2007 through 2010
Supervision practical 'Semen',	2007
Supervising 2 BSc students and 8 MSc students	2008-2011
Management skills training (2 ECTS)	
Organising WIAS Science Day	2007 and 2008
Eduation and Training Total	**54 ECTS**

Dankwoord

'Dear Ms. Hoving, I am pleased to be able to inform you that your manuscript has been accepted for publication in Animal Reproduction Science'.

Toen ik dit zinnetje las, in de zomer van 2010, waren Marc en ik in een café in Kroatië. Ik kon het niet geloven en moest Marc vragen of het echt waar was, mijn eerste artikel was eindelijk geaccepteerd! Daarna zouden er nog een aantal vergelijkbare mailtjes volgen, maar die voelden toch minder bijzonder...

Met veel plezier heb ik de afgelopen jaren aan dit brede en praktische onderzoek gewerkt. Ondanks dat het niet altijd even makkelijk was, is de eindstreep in zicht, met dit proefschrift als belangrijke mijlpaal!

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