ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

VETERINARIA 5

Reproductive Performance and Oestrous Symptoms in Primiparous Sows

Marie Sterning

SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

Reproductive performance and oestrous symptoms in primiparous sows

Marie Sterning

Akademisk avhandling, som med tillstånd av veterinärmedicinska fakulteten vid SLU för avläggande av veterinärmedicine doktorsexamen, offentligen försvaras på engelska språket i Ettans föreläsningssal, Klinikcentrum, Uppsala, fredag den 13 december 1996, kl 9.15.

Av fakultetsnämnden utsedd opponent: Professor Gary D. Dial, The University of Minnesota, College of Veterinary Medicine, Department of Clinical and Population Sciences, USA.

Abstract

The reproductive performance of primiparous sows is of great concern to pig farmers. A high percentage of the sows are culled after the first weaning due to reproductive failures. Primiparous sows often lose more weight during lactation and have a longer interval from weaning to oestrus (IWO) than older sows. The present studies were performed to provide more information about factors influencing 1) the ability to return to oestrus within 10 days of weaning, and 2) the variation in weight loss during lactation in primiparous sows kept under the same feeding regime. The oestrous symptoms were studied. Weight and backfat were checked at farrowing and at weaning and plasma progesterone was determined regularly after weaning confirming ovulation. All sows were of Swedish Yorkshire breed and were kept under the same restricted feeding regime, based on litter size, during the six weeks of lactation.

Large weight loss and to some extent large backfat loss during lactation and large litter weight gain had an unfavourable influence on the IWO. High age at pubrty was unfavourably correlated to the IWO. Short but increasing day length and a short time of boar stimulation daily after weaning had a favourable influence on the IWO.

Sows with large weight loss during lactation had a higher total disease incidence during lactation and seemed to be in a more catabolic state during late lactation than sows with small weight loss.

Daily boar stimulation after weaning and good ability to show standing reflex at puberty were both favourable for the ability to show standing reflex at the first ovulation after weaning. An increasing interval from weaning to oestrus prolonged the pro-oestrus and shortened the standing oestrus. During the season with short but increasing day length the pro-oestrus was longer than during seasons with long day length. Pigs with high

intensity and long duration of the vulvar symptoms at puberty were also more likely to have strong and long vulvar symptoms after weaning than pigs with weak and short vulvar symptoms at puberty.

Key words: weaning-to-oestrous interval, standing oestrus, pro-oestrus, vulvar symptoms, weight loss, litter size and litter weight gain, season, health, puberty

Distribution:
Swedish University of Agricultural Sciences
Department of Obstetrics and Gynaecology
S-750 07 UPPSALA, Sweden

Uppsala 1996
ISSN 1401-6257
ISBN 91-576-5229-5

Reproductive Performance and Oestrous Symptoms in Primiparous Sows

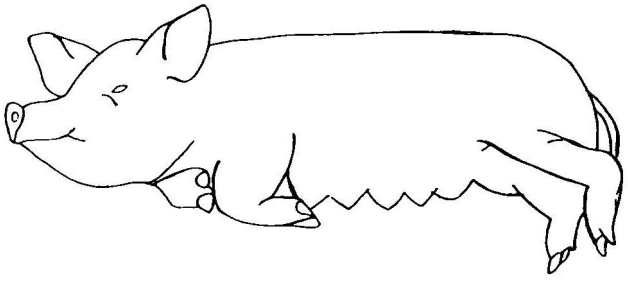
Marie Sterning
Department of Obstetrics and Gynaecology
and
Department of Animal Breeding and Genetics
Uppsala

Doctoral thesis
Swedish University of Agricultural Sciences
Uppsala 1996

Acta Universitatis Agriculturae Sueciae
Veterinaria 5

ISSN 1401-6257
ISBN 91-576-5229-5

gotab 17737, Stockholm 1996



to the wonderful sow

Abstract

Sterning, M. 1996. *Reproductive performance and oestrous symptoms in primiparous sows.* Doctor's dissertation.
ISSN 1401-6257, ISBN 91-576-5229-5

The reproductive performance of primiparous sows is of great concern to pig farmers. A high percentage of the sows are culled after the first weaning due to reproductive failures. Primiparous sows often lose more weight during lactation and have a longer interval from weaning to oestrus (IWO) than older sows. The present studies were performed to provide more information about factors influencing 1) the ability to return to oestrus within 10 days of weaning, and 2) the variation in weight loss during lactation in primiparous sows kept under the same feeding regime. The oestrous symptoms were studied during the first two oestruses after weaning. Weight and backfat were checked at farrowing and weaning and plasma progesterone was determined regularly after weaning to confirm ovulation. All sows were of Swedish Yorkshire breed and were kept on the same restricted feeding regime, based on litter size, during the six weeks of lactation.

Large weight loss and to some extent large backfat loss during lactation and large litter weight gain had an unfavourable influence on the IWO. High age at puberty was unfavourably correlated to the IWO. Short but increasing day length and a short time of boar stimulation daily after weaning had a favourable influence on the IWO.

Sows with large weight loss during lactation had a higher total disease incidence during lactation and seemed to be in a more catabolic state during late lactation than sows with small weight loss.

Daily boar stimulation after weaning and a good ability to show standing reflex at puberty were both favourable for the ability to show standing reflex at the first ovulation after weaning. An increasing interval from weaning to oestrus prolonged the pro-oestrus and shortened the standing oestrus. During the season with short but increasing day length the prooestrus was longer than during seasons with long day length. Pigs with high intensity and long duration of the vulvar symptoms at puberty were also more likely to have strong and long vulvar symptoms after weaning than pigs with weak and short vulvar symptoms at puberty.

Key words: weaning-to-oestrous interval, standing oestrus, pro-oestrus, vulvar symptoms, weight loss, litter size and litter weight gain, season, health, puberty.

Author's address: Marie Sterning, Department of Obstetrics and Gynaecology, SLU, Box 7039, S-750 07 UPPSALA, Sweden.

Contents

List of original papers

The present thesis is based on the following papers, which will be referred to by their Roman numerals **I-V**:

I. Sterning M, Rydhmer L, Eliasson L, Einarsson S, Andersson K, 1990. A study on primiparous sows of the ability to show standing oestrus and to ovulate after weaning. Influences of loss of body weight and backfat during lactation and of litter size, litter weight gain and season. Acta. vet. scand., 31: 227-236.

II. Sterning, M., Hultén, F., Holst, H., Einarsson, S. and Andersson, K., 1996. Influences of health on weight loss during lactation and on the ability to return to oestrus after weaning in primiparous sows. Submitted.

III. Sterning, M., Rydhmer, L., Einarsson, S. and Andersson, K., 1994. Oestrous symptoms in primiparous sows. 1. Duration and intensity of external oestrous symptoms. Anim. Reprod. Sci., 36: 305-314.

IV. Sterning, M., 1995. Oestrous symptoms in primiparous sows. 2. Factors influencing the duration and intensity of external oestrous symptoms. Anim. Reprod. Sci., 40: 165-174.

V. Sterning, M., Rydhmer, L., Eliasson-Selling, L., 1996. Relationships between age at puberty and interval from weaning to oestrus and between oestrous symptoms at puberty and after the first weaning in pigs. Submitted.

Offprints are published by kind permission of the journals concerned.

Introduction

During lactation sows do not normally ovulate (Kunavongkrit et al., 1982), but after weaning the follicular development starts very rapidly, culminating in standing reflex and ovulation (Rojanasthien et al., 1987). It is desired that sows return to oestrus within 7 to 10 days of weaning, but anoestrus after weaning is an important problem to the pig breeders. Among primiparous sows, only 45 to 60 per cent express their first oestrus within 7 to 10 days (Einarsson and Settergren, 1974; King, 1978; Benjaminsen and Karlberg, 1981). Multiparous sows usually have a shorter interval from weaning to first oestrus and about 77 to 92 per cent return to oestrus within 7 to 10 days of weaning (Einarsson and Settergren, 1974; King, 1978; Karlberg, 1980). It is important for the overall efficiency of a herd that each sow weans as many piglets as possible every year. In order to achieve this, the farrowing interval must not be too long, and, of course, the litter size has to be fairly large. The farrowing interval consists of the lactation period, the interval from weaning to successful mating and the gestation period. Only the lactation length and the interval from weaning to oestrus or to successful mating can be used to influence the farrowing interval. Shorter lactation length is associated with shorter farrowing interval, although the interval from weaning to oestrus can be increased (Cole et al., 1975). A short lactation period may, however, have an unfavourable effect on the litter size born or born alive in the subsequent litter (Cole et al., 1975). By shortening the lactation period from 60 days to 38 days, on average, the number of piglets produced per sow per year has been shown to increase from 16.2 to 18.9 (Aumaitre et al., 1976). In a recent study, where 89 per cent of the sows had a lactation period between 17 and 30 days, no significant relationship was found between lactation length and number of piglets born or born alive per sow per year (Xue et al., 1993). In Sweden, the lactation period is not allowed to be shorter than four weeks, making the interval from weaning to oestrus very important for the length of farrowing interval. When animals are reared in batches and all the sows in a batch are supposed to be mated within a very short period of time, it is of great importance that as many sows as possible return to oestrus rapidly after weaning. Normally sows have larger litters in parity three to five than in parity one and two. In addition, culling of the sows after the first weaning, due to anoestrus or prolonged interval to oestrus, results in economic loss and it is therefore important to identify and study factors that can influence the weaning to oestrous interval in primiparous sows.

The European wild pig is a seasonal breeder and the females are usually anoestrus during summer and autumn (Mauget, 1982). The domestic pig, on the other hand, breeds throughout the year, but the season may have an influence on the weaning to conception interval (Aumaitre et al., 1976). Sows farrowing between June and September could have a longer interval than sows farrowing during the rest of the year (Aumaitre et al., 1976). A recent study also shows that the month of weaning had a greater influence on return to oestrus after weaning in primiparous sows compared to multiparous sows (Xue et al., 1994). It would therefore be of interest

to study the influence of season on the ability to return to oestrus after weaning in Swedish primiparous sows.

Nutrition during lactation can also influence the ability to regain cyclic activity in the ovaries after the first weaning (Reese et al., 1982, 1984; King and Dunkin, 1986). For primiparous sows, lactation is a period during which metabolic adjustments are necessary to balance the high energy and protein requirements, both for milk production and for growth to a mature body weight. If the requirements exceed the feed intake, the sows will draw from their fat and protein depots (Whittemore and Yang, 1989; Mullan and Williams, 1990) which often results in excessive weight loss during lactation and extended interval from weaning to oestrus (Reese et al., 1982). The influence of weight loss during lactation on the weaning to oestrous interval in sows kept under the same feeding regime during lactation has very rarely been investigated. Recently, it was demonstrated that the heritability for weight loss in primiparous sows, kept under the same feeding regime based on litter size, is fairly large (0.4) (Rydhmer et al., 1992).

As reviewed by Booth (1990), nutrition and metabolic status may influence the reproductive function of the sow. The biochemical and endocrinological bases of the interrelationship between the hypothalamic-pituitary-gonad axis, and fat and protein metabolism are as yet poorly defined. The variation in weight loss during lactation may be due to individual differences in appetite or, as recently indicated by Rojkittikhun et al. (1992), in the regulation of energy metabolism during lactation. It would also be of interest to study the relationships between health during lactation and at weaning and both weight loss during lactation and the ability to return to oestrus after weaning in sows kept under the same feeding regime. The influence of health on the interval from weaning to oestrus is very poorly studied, although in swine practice illness is suspected to contribute to a delay in the onset of oestrus after weaning.

Post-weaning anoestrus in sows is not always identical with a delay in resumption of ovarian activity. Both in gilts (Einarsson et al., 1974; Eliasson, 1989) and in primiparous sows (Benjaminsen and Karlberg, 1981) ovulation has been shown to occur without a detectable standing reflex. A higher percentage of both gilts (Signoret, 1970) and sows (Schenk, 1967) express external oestrous symptoms such as standing reflex upon physical contact with a boar than gilts and sows not having any physical boar contact. It would be of interest to investigate the occurrence of ovulation without a detectable standing reflex among Swedish primiparous sows.

Very few studies have been performed on oestrous symptoms in sows. Burger reported in 1952 that pro-oestrus (swelling of the vulva) lasted for 3.3 days, but this investigation included both gilts and sows. Strong oestrous symptoms in sows are important for optimum timing of the mating or insemination. When the batch farrowing system is used and the sows are group-housed during gestation, it is

important to detect as many sows in oestrus as possible within the mating period in order not to split up the group of sows.

More knowledge is required about the duration and intensity of the oestrous symptoms in primiparous sows, and about factors influencing these symptoms, in order to improve them. It is known from studies on gilts that the vulvar symptoms (reddening and swelling) differ with oestrous number and that there are significant positive correlations between the duration and intensity of the oestrous symptoms at the first three oestruses (Eliasson, 1989). Low backfat thickness at 90 kg live weight had an unfavourable influence on the duration and intensity of the vulvar symptoms compared to high backfat thickness (Eliasson, 1991). A recently published study on gilts (Rydhmer et al., 1994) also showed that the heritability for the ability to show standing reflex and for the duration and intensity of the oestrous symptoms at puberty seems to be high enough to allow for successful selection to improve the oestrous symptoms. It is therefore of great interest to study whether selection for distinct and strong oestrous symptoms at puberty will improve the oestrous symptoms after the first weaning.

Aims of the study

The aims of the present work on primiparous sows kept under the same feeding regime, based on litter size, were to study:

- the ability to show standing reflex and to ovulate after weaning;

- relationship between the ability to return to oestrus after weaning and a) loss of weight and backfat thickness during lactation, b) litter size, c) litter weight gain, and d) season;

- relationship between health during lactation and at weaning and a) the weight loss during lactation and b) the ability to return to oestrus after weaning;

- relationship between blood parameters that could reflect metabolic state during late lactation and a) weight loss during lactation and b) the ability to return to oestrus after weaning;

- duration and intensity of the oestrous symptoms at the first and second oestrus after weaning;

- relationships between the duration and intensity of the oestrous symptoms and a) interval from weaning to oestrus, b) loss of body reserves (weight and backfat) during lactation, c) body reserves at weaning, d) litter size and litter weight gain and e) season;

- relationship between age at puberty and interval from first weaning to oestrus;

- relationship between duration and intensity of the oestrous symptoms at puberty and after the first weaning.

Material and methods

Animals

All animals, included in the five papers in the thesis were pure-bred Swedish Yorkshire pigs from the research herd at Funbo-Lövsta, belonging to the Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences, Uppsala, Sweden. The studies on the sows were carried out from April 1984 to September 1992. All sows were also included in a selection experiment for improved lean tissue growth rate (25-90 kg) on two different protein levels (two selection lines) (Stern et al., 1993). The animals were reared in batches and each generation included three batches. Altogether 21 batches were included in the five papers in the thesis. The first six batches were base populations in the selection experiment. Batches number 7-18 were selected for improved lean tissue growth rate and the last three batches were randomly selected (Stern et al., 1995). Papers number I, II, III, IV, and V included pigs from batches number 1-9, 11-21, 11-15 and 19, 11-15 and 19-21, and 1-21, respectively.

General management

All units in the research herd were kept indoors. The pens had a concrete floor and once daily a small amount of straw was placed in the pen. Vaccination/prophylactic treatment routines were used regularly in all pigs against erysipelas, parvovirus infection, and endo- and ectoparasites. The pigs were weaned at 6 weeks of age and stayed in the farrowing pen until about 10 weeks of age when they were moved to the rearing units. Six gilts were kept in each pen. At the end of the rearing period, at about 190 days of age, the gilts were relocated to a breeding unit, in which 4 animals were kept in each pen. Adult boars were also present in this unit. Before mating the gilts were moved to the gestation units where boars were always present, still with 4 gilts in each pen. The gilts in one batch were all mated during a four-week period. Due to the design of the selection experiment the gilts were rather old at mating (on average about 310 days, ranging from 250 to 385 days). The oestrus of mating ranged from the 1st to the 9th. Three weeks before expected farrowing the gilts were moved to individual farrowing pens. The lactation period was 6 weeks. The sows were weighed and ultrasonic measurement of the backfat was made within two days of farrowing and weaning (no sow was weighed before farrowing). Measurement of the backfat was made at the last rib on both sides, approximately 8 cm from the middle of the back. The piglets were weighed at birth and at three and six weeks of age. After weaning the sows were moved back to the gestation units. The mating period, of four weeks, started approximately two weeks after the beginning of the weaning period. Due to this the sows were mated either on their first or second oestrus after weaning.

Feeding regimes

From 25 to 90 kg live weight the pigs were group-fed twice daily, according to a standard feeding regime (Simonsson, 1988). One selection line had a diet with a high protein level (18.5% crude protein, 0.96% lysine) and the other selection line

a diet with a low protein level (13.1% crude protein, 0.64% lysine) (Stern et al., 1993). The energy level was 11.9 MJ/kg in both diets. The total amount of energy offered was the same for both lines. The feeding scale was adjusted once a week according to the average live weight in each pen. In the last three batches both selection lines were fed a commercial diet for growing finishing pigs (12.2 MJ/kg, 16.5% crude protein, 0.85% lysine) (Stern et al., 1995). From 90 kg live weight until farrowing the gilts were fed 2.2 kg/day of a barley-based sow diet (12.1 MJ/kg, 14.5% crude protein). After farrowing the feed allowance was gradually increased from 2.0 kg at farrowing to a maximum of 2.0 kg + 0.4 kg per piglet. After weaning the daily feed intake was 4-5 kg until mating and thereafter 2.2 kg.

Oestrous detection

At puberty: From 160 days of age until all oestrous symptoms had ceased at puberty (the first ovulation) the gilts were checked twice daily for oestrous symptoms by inspection of the vulva and checking of the standing reflex, by back pressure test (Eliasson, 1991). Specially trained technicians carried out these recordings, except during weekends when the ordinary staff performed these recordings. A boar was walking around in all the pens once daily to stimulate the gilts and for the purpose of oestrous detection, especially in gilts not reacting to the back pressure test. The boar was introduced when all the gilts in a pen had reached 150 days of age. The recording of the oestrous symptoms continued until all reddening and swelling had ceased at puberty. Blood samples for progesterone determination were drawn every 10 days from 170 days of age until the first oestrus and approximately 12 days after the first oestrus. The duration of the oestrous symptoms was recorded and the intensity of the reddening and swelling of the vulva was scored as no, weak or strong.

After weaning: The sows were treated in two different ways with regard to oestrous detection after weaning. In batches 1-10 and 16-18 standing reflex was checked once daily, using the back pressure test, by the ordinary staff. The interval from weaning to first oestrus was recorded. Blood samples for determination of plasma progesterone were drawn either at 12 days after weaning, if no standing oestrus was recorded within 10 days of weaning, or 12 days after the first standing oestrus, if this occurred within 10 days of weaning. In batches 11-15 and 19-21, the oestrous symptoms were checked twice daily from the day after weaning, by inspection of the vulva and detection of standing reflex, using the back pressure test. Specially trained technicians carried out these recordings, except during weekends when the ordinary staff performed the recordings. A boar was present during the morning inspection to stimulate the sows and for the purpose of oestrous detection, especially in sows not reacting to the back pressure test. Due to the design of the pens the boar could not always be in the same pen as the sow during the inspection, but he could reach the sow with his snout through the fence. The recording of the oestrous symptoms continued until all reddening and swelling of the vulva had ceased at the oestrus of mating, but not later than at the second oestrus after weaning. Blood samples for determination of plasma progesterone were drawn every 7 days after weaning until the first standing oestrus and 12 days

after the first standing oestrus. The intensity of the reddening and swelling of the vulva was scored as no, weak, moderate or strong.

The following definitions were used both at puberty and after the first weaning:

Pro-oestrus:	the period before standing oestrus when reddening and swelling of the vulva occur.
Standing oestrus:	the period when the pig exhibits the standing reflex.
Duration of reddening and swelling of the vulva:	the period before, during and after the standing reflex when reddening and swelling of the vulva occur.

The ability to show standing reflex was scored as no standing reflex (0) or standing reflex (1).

Season

The effect of weaning season on the ability to return to oestrus after weaning (papers I and IV) and on the oestrous symptoms (paper IV) were analysed by dividing the year into four seasons, based on total and increasing or decreasing day length. The dates of the seasons were the following: 1: 21/12-20/3; 2: 21/3-20/6; 3: 21/6-20/9; 4: 21/9-20/12. The mean day length was around 18 h in June and between 6 and 7 h in December (cf: Ehnvall et al., 1981).

Disease during lactation

Occurrence of clinical disease during the lactation period was recorded in the study presented in paper II. When labour had to be manually assisted, or if oxytocin was injected to improve labour and/or milk let-down this was recorded as *farrowing disorder*. Rectal temperature was checked in sows showing signs of illness and if the temperature exceeded 39.5°C fever was recorded. *Fever after farrowing* means fever occurring within two to three days of farrowing in relation to infections around farrowing, whereas *fever* means fever occurring later during lactation. When feed intake ceased or was greatly reduced for a few days during lactation, *lack of appetite* was recorded. Farrowing disorders were diagnosed and recorded by the stable staff, whereas other diseases were diagnosed and treated by veterinarians.

Clinical health examination

On the day of weaning (± 1 day) a clinical health examination was performed by two veterinarians examining 6 and 2 batches each (paper II). *Body temperature* was recorded. Body condition (fatness and muscle volume) was recorded after a subjective visual examination and by palpation of the bone, muscle and fat tissues at the scapula, ribs and the lumbar vertebras (loin). Based on this examination, a *condition score* was given to each sow, ranging from 1 (very thin) to 5 (fat). *Appetite* on the day of weaning was recorded as *normal* if the sow ate the entire daily feed ration without delay otherwise it was considered to be *reduced*. *Locomotor disorders*, which include difficulty rising, lameness and abnormal walk (stiffness or an abnormal swaying gait) were recorded by allowing the sow to walk

freely about 10-20 meters, on a concrete floor. *Leg remarks* included *joint remarks* (one or several swollen joints occasionally with discoloration and pain or exostosis), *abscesses* on the legs and/or on the scapula, *hoof injuries* (cracks and signs of infection) and *other observations* (bursitis and different skin wounds). If a diffuse increase in the density and oedema of the *mammary glands* was found, occasionally with discoloration and pain, *signs of acute mastitis* were recorded. Focal increase in the mammary gland density without any oedema or pain was recorded as *signs of chronic mastitis*. The number of mammary glands with *wound on teats* or mammary skin was recorded. A sow could have several different remarks on the mammary glands and on the legs.

Blood sampling and analyses

All blood samples were collected by puncture of the jugular vein, on restrained animals, using vacutainer tubes with additives of heparin, EDTA, or without additive, depending on the requirements for the analyses.

The plasma levels of progesterone (papers I-V) were determined using a radioimmunoassay system (Bosu et al., 1976). The system was designed to cover a wide range of high progesterone levels, thereby sacrificing in part the sensitivity of the assay. In this assay system a progesterone concentration of > 7 nmol/L indicates active luteal tissue in the ovaries (Eliasson, 1989). After centrifugation the plasma was removed and stored at 20°C until assayed (within two months).

Haemoglobin (B-HGB), packed cell volume (B-PCV) and total white blood cells (B-WBC) (paper II) were determined in an automatic cell counter (Sysmex F-800; TOA Medical Electronics, Japan). Serum concentrations of urea, creatinine, triglycerides, free fatty acids (FFA) and protein (paper II) were determined using a Cobas Mira multichannel analyser (Roche, Basle). Serum urea was quantified with the urease-glutamic dehydrogenase reaction (Eisenweiner,1976), and creatinine with the Jaffe reaction at 500nm (Fabiny and Ertinghausen,1971). Triglycerides and FFA were determined with enzymatic colorimetric methods. Triglyceride concentration was determined on the basis of the glycerol content (Megraw et al., 1979). Concentration of FFA was determined by its ability to acylate coenzyme A in the presence of CoA-synthetase (Duncombe,1964). Total protein concentration was determined spectrophotometrically using the biuret method. Serum proteins were separated by agaros gel electrophoresis.

Statistical analyses

Analyses of variance and correlation were performed on data using the Statistical Analysis System (SAS Institute Inc., 1985-1987). All effects in the statistical models, except for the residual random term (papers I-V) and for the random effect of animal in the genetic analyses (paper V), were regarded as fixed. Differences in frequencies between classes of sows were analysed using the chi square test (papers I, II and V). Genetic parameters (paper V) were estimated using REML analyses with a multivariate procedure (Johansson, 1992). The following levels of significance were used: N.S., $P>0.05$; * $P\leq0.05$; ** $P\leq0.01$; *** $P\leq0.001$.

Summary of investigations presented

The ability to show standing reflex and to ovulate after weaning (papers I-IV)

The ability to show standing reflex and to ovulate within 10 days of weaning (SO) varied on average, from 60.0 to 87.4 per cent (papers I - III). The best results were achieved when all sows were boar-stimulated once daily after weaning and the average weight loss during lactation was low (paper III).

Ovulation without a detectable standing reflex within 10 days of weaning (O) varied from 1.7 to 11.7 per cent (papers I and III). The lowest frequency was recorded when a boar was present during the morning inspection and the oestrous symptoms were recorded by specially trained staff (paper III). When a high frequency of sows did not show standing reflex at the first ovulation after weaning, the distribution of the interval from weaning to first detected standing oestrus had two peaks, the second around 25 days after weaning (paper I). In study I there was a high frequency of O sows among the animals weaned during the spring. When boar stimulation was used the total frequency of O sows was very low and the difference between season could not be analysed (paper IV).

Standing reflex without ovulation within 10 days of weaning (S) varied from 0.6 to 3.9 per cent (papers I and III). The lowest frequency again being when a boar was used for stimulation and detection of oestrus and when specially trained personnel recorded the oestrous symptoms.

Sows neither showing standing reflex nor ovulating within 10 days of weaning (NSO) had higher body weight and backfat losses during lactation and had lower weight and backfat thickness at weaning than SO sows (paper I). The difference in weight and backfat losses between NSO and SO sows was smaller and not significant when the frequency of SO sows increased (papers II and IV). Among SO sows, boar stimulated or not, there were significant positive correlations between a) body weight loss during lactation, b) litter weight gain and the interval from weaning to oestrus (IWO) (papers I and IV). Litter size was positively correlated to IWO, but significant only for sows not boar stimulated after weaning (papers I and IV). Sows weaned in the season with short but increasing day length had the highest frequency of SO animals (papers I and IV). No significant decrease in the frequency of SO sows could be found during late summer and autumn.

There was no difference in the total disease incidence during lactation between SO and NSO sows. The frequency of the different diseases did not differ significantly, although mastitis seemed to be more common among NSO sows than among SO sows (paper II). Very few differences were found in the clinical health at weaning between SO and NSO sows. There was, however, a numerical difference in the condition score, NSO sows being thinner on average than the SO sows (paper II). Blood analyses indicated that NSO sows might have more trouble with subclinical infections during late lactation than the SO sows. No significant differences in the

blood parameters reflecting the metabolic state could be found during late lactation between SO and NSO sows.

Relationships between health during lactation and at weaning, and the weight loss during lactation (paper II)

The total disease incidence during lactation was higher among sows with large relative weight losses (RWL) compared to sows with small RWL. The incidence of different types of diseases also differed. Farrowing disorders (problems with labour or milk let-down) was the most common disease in sows with small RWL, whereas mastitis was the most common disease in sows with large RWL.

The most obvious differences in clinical health on the day of weaning between sows with small or large RWL related to condition score and appetite. Among sows with large RWL a higher frequency were thin at weaning and a higher frequency had reduced appetite on the day of weaning, compared to sows with small RWL. No differences indicated that infections or injuries were more common in sows with large RWL than in sows with small RWL. Blood analyses from a sample drawn one week before weaning indicated that subclinical infections in late lactation were not more common among sows with large RWL than in sows with small RWL.

There were significant negative correlations between RWL and a) concentration of haemoglobin and b) packed cell volume. The metabolic parameters showed that catabolism was more pronounced in late lactation among sows with large RWL than in sows with small RWL, although only significant for the concentration of triglycerides.

Oestrous symptoms (papers III and IV)

The mean duration of both pro-oestrus and standing oestrus was 2.0 days at the first oestrus after weaning and 13.3 per cent of the sows did not show any pro-oestrus (paper III). There was a significant positive correlation between the duration and the intensity of the vulvar symptoms (reddening and swelling of the vulva) (paper III). At the second oestrus after weaning, pro-oestrus was longer (3.1 days), the frequency of sows not showing any pro-oestrus was lower (1.8%) and the vulvar symptoms were more intense than at the first oestrus (paper III). The duration of the standing reflex did not differ significantly between the first and second oestrus (paper III). The individual sow **repeated her pattern** with regard to the intensity of the vulvar symptoms from the first to the second oestrus as well as to the duration of the first and second pro-oestrus (paper III).

There were significant positive correlations between IWO (3-10 days) and the interval from weaning to the first pro-oestrus, and the duration of the first pro-oestrus (paper IV). The duration of the first standing reflex was negatively correlated to the IWO (3-10 days) (paper IV). The intensity of the vulvar symptoms was not influenced by the IWO.

Neither body weight nor backfat thickness at weaning or at oestrus influenced the duration or intensity of the oestrous symptoms significantly. Most of the correlations between body weight and backfat losses during lactation and the duration and intensity of the oestrous symptoms were negative but not significant (paper IV). The percentage of sows showing no pro-oestrus at the first oestrus after weaning increased with increasing litter size. There was also an unfavourable influence on the duration and intensity of the vulvar symptoms by increasing litter size (paper IV).

There was little influence of season on the duration and intensity of the oestrous symptoms. The duration of pro-oestrus was, however, significantly shorter in the second and third season, with long day length, than in the first season, with short but increasing day length. Neither the duration of standing reflex nor the intensity of the vulvar symptoms were significantly influenced by the season (paper IV).

Relationships between age at puberty and the interval from first weaning to oestrus and between the oestrous symptoms at puberty and after the first weaning (paper V)

Pigs that were younger at puberty had a shorter interval from first weaning to oestrus than pigs that were older at puberty. Positive genetic and phenotypic correlations were found between age at puberty and interval from weaning to first detected standing oestrus. Age at puberty was negatively correlated, both genetically and phenotypically, to the ability to show standing oestrus and to ovulate within 10 days of weaning. Among pigs not showing standing reflex at puberty (the first ovulation), the frequency of animals not showing standing reflex at ovulation within 10 days of the first weaning was higher than among pigs showing standing reflex at puberty. There was a significant positive correlation between the total duration and intensity of the vulvar symptoms at puberty and at the first oestrus after weaning. No relationship was found between the duration of standing reflex at puberty and after the first weaning.

General discussion

A long interval from weaning to first ovulation results not only in a longer farrowing interval, but may also result in a smaller subsequent litter. As shown in several studies, sows mated or inseminated around 6 to 9 days after weaning have a smaller subsequent litter than sows mated earlier after weaning (Dewey et al., 1994; Vesseur and Kemp, 1993; Sterning and Lundeheim, 1995). Many factors can influence the resumption of ovarian activity after weaning, as will be discussed later.

A long interval from weaning to oestrus, recorded in practice, is not always equal to a delay in the resumption of ovarian activity. By using post-mortal examination of the ovaries (Einarsson et al., 1974) or frequent blood sampling for detection of plasma progesterone (Eliasson, 1989; papers I and III), it has been shown that ovulation without a detectable standing reflex occurs in both gilts and sows. It is also possible to examine the ovaries using laparoscopy (Andersson et al., 1984) or transrectal ultrasonography (Soede et al., 1992; Dalin et al., 1995; Mburu et al., 1995). For more practical applications, it is also possible to analyse progesterone metabolites in the faeces (Hultén et al., 1995).

In herds where there is a problem with long intervals from weaning to the first detected oestrus, the possibility of both delayed resumption of the ovarian activity and a high frequency of sows not showing standing reflex at the first ovulation after weaning (O) has to be considered. If the distribution pattern of the interval from weaning to first detected oestrus has two peaks, the problem may be a high frequency of O sows (Benjaminsen and Karlberg, 1981; paper I). The second peak usually occurs between 24 and 30 days of weaning, if the O sows ovulated within 10 days of weaning.

When ovarian activity is normal after weaning but no oestrus is detected, it is possible that the oestrous symptoms are weak or missing but it is also possible that the oestrous detection is inadequate. No reddening or swelling of the vulva around oestrus has been shown to occur in primiparous sows (paper III). Eliasson (1989) showed that ovulation can occur in gilts without standing reflex and vulvar symptoms, although at a very low rate. It was, however, more common for vulvar symptoms to be recorded around ovulation, although a standing reflex could not be detected. Factors that may influence the sows' ability to express oestrous symptoms or factors that can facilitate detection of oestrous symptoms will be discussed later.

In studies where progesterone determination has been used to confirm ovulation, standing reflex without ovulation (S) has been shown to occur, although at a very low frequency, in both gilts (Eliasson, 1989) and sows (papers I and III). In gilts this was associated with weak vulvar symptoms but not necessarily with an irregular interval between oestruses (Eliasson, 1989). In the present study

(paper I), the frequency of S sows, within 10 days of weaning, was 3.9 per cent, but in paper III, where the sows had physical boar contact and oestrous detection was performed carefully, only one sow (0.6%) was recorded as a S sow. The difference in the frequency of S sows between paper I and paper III may indicate that careful oestrous detection using a boar would show these sows as not being in oestrus and a number of infertile inseminations could therefore be avoided. However, this is probably not a major problem in swine practice, but could still lead to non-fertile inseminations. A far more common cause of infertile insemination is probably insemination at the wrong time, due to lack of knowledge about oestrous symptoms and oestrous detection.

Factors influencing the resumption of ovarian activity after weaning

The interval from weaning to first oestrus with an ovulation, in practice referred to as the interval from weaning to oestrus, can be influenced by many factors in primiparous sows. As the mean interval from weaning to oestrus could be greatly influenced by a few very long intervals, a better indicator of sow performance may be obtained by using the percentage of sows in oestrus within a certain time after weaning. This method has been discussed by Xue et al. (1993) and has been used in papers I to V.

In the present study, all sows had a lactation period of six weeks. A short lactation period may result in a prolonged interval from weaning to oestrus compared to a longer lactation period (Cole et al., 1975). A lactation period of more than three weeks did not, however, reduce the weaning-to-service interval much further (Xue et al., 1993). A short lactation period may also have an unfavourable influence on the subsequent litter size, but a lactation period of more than three to four weeks does not normally increase the litter size further (Cole et al., 1975; Dewey et al., 1994). In Sweden a lactation period shorter than four weeks is not allowed. The results from the present investigations, using six weeks of lactation, could therefore be used for practical applications in Swedish commercial farms.

Many studies have shown that the nutrition level during lactation has a major influence on the body reserves of the sow and on the interval from weaning to oestrus. Very few investigations, however, have studied the influence of weight and backfat loss on the interval from weaning to oestrus in sows kept under the same feeding regime. Using the same restricted feeding regime based on litter size, sows showing standing reflex and ovulating within 10 days of weaning (SO) lost less weight and backfat thickness during lactation and were heavier with thicker backfat at weaning than sows neither showing standing reflex nor ovulating within the same time (NSO) (paper I). These differences were not as obvious when the percentage of SO sows was high (paper II), but both in paper I (60.0% SO sows) and paper III (87.4% SO sows) there was a significant correlation between weight loss during lactation and the interval from weaning to oestrus among SO sows. A direct comparison with other studies has not been possible, as most of them have used different feeding regimens to attain differences in the loss of body weight and

backfat thickness. As Aherne and Kirkwood reviewed (1985) it has been shown that high-fed sows losing less weight during lactation had a shorter interval from weaning to oestrus than low-fed sows losing more weight. It has been indicated that primiparous sows with large weight loss during lactation are in a more pronounced and prolonged catabolic state than sows with small weight loss (Rojkittikhun et al., 1993b). In the present study a blood sample was drawn after five weeks of lactation (paper II). The analyses indicated that sows showing large relative weight loss during lactation seemed to be in a more catabolic state than sows showing small relative weight loss. There were, however, no significant differences in the metabolic parameters a week before weaning between SO and NSO sows (paper II).

The metabolic state of the sow during lactation has an important influence on the reproductive performance after weaning (reviewed by Foxcroft et al., 1996). It has been suggested that inadequate nutrient or energy intake during lactation influences either the releasable pools of LH or the hypothalamic pulse generator (Armstrong and Britt, 1987). Insulin is thought to be one factor mediating the influence of metabolism on the LH secretion (Foxcroft et al., 1996). Changes in the ovarian sensitivity to gonadotrophic stimulation may also be important for the reproductive response to changes in the metabolic state (Foxcroft et al., 1996). In a study where the energy intake was either high or low during the entire lactation period of three weeks or reduced for one week during lactation it was shown that the interval from weaning to oestrus was reduced in sows with low energy intake during the entire lactation period or for just one week (first, second or third week) compared to sows with high energy intake during the entire lactation period (Koketso et al., 1996). Concentrations of insulin and glucose were influenced by the energy intake and insulin and glucose concentrations and the pulse frequency of LH differed on day 21 of lactation between sows returning to oestrus within seven days of weaning and sows returning to oestrus after more than seven days (Koketso et al., 1996). The process of follicular development occurs over several weeks and thus the process starts during lactation in sows returning to oestrus early after weaning (Foxcroft et al., 1996). The catabolic state of the sow during lactation could have an important influence on the imprinting of follicles that will enter the final stage of maturation after weaning (Foxcroft et al., 1996). This could be important for the sow fertility after weaning (Foxcroft et al., 1996). As discussed by Foxcroft et al. (1996) the metabolic state of the sow during late gestation also becomes very important when very early weaning is used. In practice, it is important to avoid large weight loss and pronounced catabolism during the first lactation period. As will be discussed later it is possible to reduce weight loss in primiparous sows by selection.

There is a strong correlation between litter size, litter weight gain and body weight loss of the sow during lactation (Danielsen and Nielsen, 1982). Litter size could therefore have an indirect effect on the interval from weaning to oestrus or on the percentage of SO sows. However, no significant differences in litter size or litter weight gain could be found between NSO and SO sows in the present study

(papers I and II), but there was significant correlation between the litter weight gain and the IWO (papers I and IV). In practice, especially in primiparous sows, it may be favourable for the reproductive performance to reduce the number of piglets in very large litters in order to avoid excessive body weight loss during lactation.

A short time of physical contact with a mature boar daily has been shown to decrease the age at puberty in gilts (Brooks and Cole, 1970; Karlbom, 1982) and the IWO in sows (Pearce and Pearce, 1992), but there are also reports indicating that exposure to a mature boar after weaning does not increase the number of primiparous sows in oestrus within 10 days of weaning (Dyck, 1988). A comparison of the results from paper I and III indicates that daily boar contact after weaning increases the number of SO sows (60.0 and 87.4%, respectively). The sows in paper I, however, lost more body weight, on average, than the sows in paper III, which may also have contributed to the result. A short period of physical contact with a mature boar daily after weaning could be used in practice when trying to reduce the average IWO in a herd.

In the present study, weaning season had an influence on the frequency of SO sows. Both in paper I and paper IV the highest frequency of SO sows was found between December 21 and March 20 (short but increasing day length). A decrease in the percentage of SO sows was seen between September 21 and December 20 in paper I (short and decreasing day length) compared to other seasons, but the difference was not so obvious in paper IV. The difference in the results between paper I and paper IV could be explained by the fact that boar stimulation decreases the seasonal response in sows, as shown by Booth and Baldwin (1983). They reduced the boar influence by ablation of the olfactory bulbs which rendered the sows much more responsive to seasonal influence. Another Scandinavian study showed that the percentage of primiparous sows ovulating within 10 days of weaning was lower from July to December than from January to June (Benjaminsen and Karlberg, 1981). A North American study showed that both the farrowing rate in sows bred during December or January were higher than in sows bred during July or August and the IWO was shorter in sows weaned between November and January compared to sows weaned between June and August (Xue et al., 1994). It has also been shown that primiparous sows have greater seasonal variability in IWO compared with multiparous sows (Xue et al., 1994). The influence of season is probably due, in part, to the total and also increasing or decreasing day length. The photo periods are known to influence the age at puberty in gilts (Paterson and Pearce, 1990) and the pubertal development in boars (Andersson et al., 1996). In some countries, seasonal infertility is a problem in late summer and autumn. The most important aspect of this infertility is reduced farrowing rate (Stork, 1979; Love, 1981), but an increase in the IWO has also been shown in a minority of sows (Hurtgen et al., 1980). The influence of photo periods can be mediated by the hypothalamo-pituitary-gonadol response to changes in the diurnal profile of melatonin secretion, as reviewed by Love et al. (1993). The seasonal increase in IWO could also be mediated through high ambient

temperature during summer and autumn. High temperature could cause a decrease in appetite and hence an increase in the weight loss during lactation and a longer IWO (Prunier et al., 1994; Prunier et al., 1995). In Scandinavian countries, pig producing units have to consider the possibility that the IWO may be shorter and the percentage of primiparous sows in oestrus within 7 to 10 days of weaning higher during a season with short but increasing day length, compared to other seasons. There could also be an increase in the IWO during late summer and autumn; however, less pronounced if daily boar stimulation after weaning is used. If the temperature is very high during the summer there could be a decrease in the reproductive performance due to a decrease in appetite.

In swine practice illness is suspected of being one factor that may increase the IWO. Andersson et al. (1984) showed that in one gilt which developed limb weakness immediately before the fourth pro-oestrus, the ovarian activity ceased after three successive oestruses. The gilt had slight vulvar symptoms, but failed to show standing reflex. Laparoscopy revealed no signs of ovulation and within a few weeks the ovaries became small with only small follicles and remnants of old corpora lutea visible. However, very few other investigations have studied the relationship between health and ovarian activity. In the present study no important significant differences in disease incidence during lactation or in clinical health at weaning between SO and NSO sows could be found (paper II). The incidence of mastitis during lactation, however, seemed to be somewhat greater among NSO sows than among SO sows. Persson et al. (1989), showed in a long-term study on health status, that agalactic sows did not have a significantly longer IWO than non-agalactic sows. NSO sows had significantly higher total white blood cell counts and γ-globulin concentrations than SO sows a week before weaning (paper II). This could indicate that sub-clinical infections were more common among NSO sows than among SO sows. It is, however, not possible to conclude from the present study, whether health status has a direct influence on the IWO or on the ability to return to oestrus within 10 days of weaning or not. Fahmy (review, 1981) reported on four investigations where the administration of antibiotics was not found to reduce the IWO significantly. The antibiotics were, however, administered after weaning and could therefore not have changed the influence of an sub-clinical infection on the reproductive axis during lactation. More research is needed to understand fully the relationship between health and IWO or ovarian activity. As the disease incidence was shown to be higher among sows with large weight loss during lactation compared to sows losing less weight (paper II) disease during lactation may possibly have an indirect influence on the IWO, mediated by the loss of body reserves and the catabolic influence on the metabolism. Good health during the first lactation may therefore be beneficial both to the sows' body reserves and the IWO. The general health status of the sows in the research herd at the time of the present investigations was considered to be good (Arne Persson, personal communication). The herd was free from serpulina infections and the clinical appearance of diseases of the respiratory tract was low. Very little clinical evidence of ecto- or endo-parasites was seen. Occasionally, the herd had problems

with proliferative haemorrhagic enteropathy (PHE), as described by Hultén et al. (1991).

The heritability for age at puberty (first ovulation or first standing oestrus) has been shown to be fairly high, around 0.3 (Rydhmer et al., 1994; Bidanel et al., 1996). Recent studies have also shown that the heritabilty for the IWO (0.2-0.3) in primiparous sows is high enough for successful selection (paper V; Ten Napel et al., 1995). It has been shown that selection for low age at puberty not only had a favourable effect on the interval from weaning to oestrus (Holder et al., 1993) or to mating (Merks and Molendijk, 1995), but also resulted in a higher frequency of sows completing five parities (Holder et al., 1993). The present study also revealed a high genetic correlation between age at puberty and both the IWO (0.45) and the ability to return to oestrus within 10 days of weaning (-0.5) (paper V). In addition, when dividing the pigs into the three classes young, medium or old at puberty, a significantly higher frequency of SO pigs was found in the young class than in the other classes (paper V). One possible way of reducing the problem of the long IWO among primiparous sows could therefore be to only use gilts with a low age at puberty for breeding. Although management factors have a large effect on reducing the IWO, no pig will express a better reproductive performance after the first weaning than its genetic capacity allows.

Factors influencing the ability to express oestrous symptoms

As discussed earlier, ovarian activity can be associated with lack of or weak to normal oestrous symptoms. It is important to have good knowledge about oestrous symptoms and factors that may influence them. Only then it is possible to give sows the best opportunity to express their oestrous symptoms and to perform good oestrous detection. A period of reddening and swelling of the vulva before the standing oestrus makes it easier to detect sows that are close to oestrus.

Careful oestrous detection and good knowledge of oestrous symptoms could increase the frequency of sows detected with oestrus at the first ovulation after weaning (compare paper I and paper III). The degree of fear and stress in sows, in response to the human attitude and behaviour has actually been shown to influence the reproductive performance of sows unfavourably (reviewed by Hemsworth and Coleman, 1996) and is probably of importance for good oestrous detection.

Some of the oestrous symptoms differ in duration and intensity between the first and second oestrus after weaning. The pro-oestrus has been shown to be significantly shorter at the first oestrus after weaning compared to the second oestrus (paper III). The frequency of sows not showing pro-oestrus was also higher at the first than at the second oestrus after weaning (paper III). A fairly high repeatability value for the duration of the two pro-oestrus periods indicates that the individual sow has similar duration of the first and second pro-oestrus, although the second pro-oestrus may be a little longer than the first, as has been discussed earlier (paper III).

Repeatability values also showed that the individual sow has about the same intensity of vulvar symptoms at the first and at the second oestrus after weaning. On average, both the duration and intensity of the vulvar symptoms increase from the first to the second oestrus. The total duration and the intensity of the vulvar symptoms are also positively correlated within oestrus. The average duration of the standing oestrus was 2.0 days and did not change with oestrous number in the present investigation (paper III). The duration is in agreement with the result on primiparous sows found by Nogueira et al. (1984). There was little variation in the duration of the standing oestrus in the present investigation as it was measured in days (papers III-V). About 70 per cent of the sows had a standing oestrus of 2 days (paper V).

The present investigations show that the IWO influences both the duration of pro-oestrus and the duration of standing oestrus (paper IV). The interval from weaning to the elevation of plasma oestradiol-17β has been shown to be prolonged and the interval from the rise in oestradiol-17β to the onset of standing oestrus tended to be longer in sows with a longer interval from weaning to oestrus (IWO) than in sows with a shorter IWO (Rojkittikhun et al., 1993a). The duration of pro-oestrus increases with an increasing IWO (within the range 3-9 days) (paper IV). These two studies indicate that the duration of pro-oestrus is related to the plasma oestrogen levels. Andersson et al. (1984), however, showed in a study on gilts that although the duration of elevated oestrogen levels did not change with oestrous number, the duration of pro-oestrus was shortened. Oestrogen receptors have been found in the sex skin of female monkeys (Ozasa and Gould, 1982) and in the cervix, oviduct and uterus of gilts (Stanchev et al., 1984, 1985, 1990), and are believed to mediate the changes during the oestrous cycle. Most probably, these receptors also exist in the vulva of the female pig. Andersson et al. (1984) suggested that the receptor mechanism in the vulva or the sensitivity to oestrogen might change with oestrous number in the gilt. The duration of standing oestrus decreased with an increasing IWO, within the range 3 to 9 days (paper IV). The duration of the standing reflex is important for the time of ovulation. Soede et al. (1992) and Mburu et al. (1995) have shown that ovulation occurs within a mean of close to 70 per cent of the standing oestrous period. Consequently, sows with a longer standing oestrus ovulate later from the start of the standing reflex, on average, than sows with a shorter standing oestrus. Lower farrowing rates (Vesseur and Kemp, 1993, Sterning and Lundeheim, 1995) and smaller subsequent litter size (Vesseur and Kemp, 1993; Dewey et al., 1994) in sows with a longer IWO (at least within the range 3 to 9 days) could be caused by the shorter standing oestrus and the subsequent suboptimal insemination time, if normal insemination routines are used (Kemp and Soede, 1996). A short standing oestrus increases the risk of inseminating too late.

As discussed earlier, a short period of boar contact daily after weaning can reduce the IWO. In addition, the frequency of pigs showing standing reflex at ovulation has been shown to increase if a boar is used for oestrous detection (Schenk, 1967; Signoret, 1970; compare papers I and III). As reviewed by Morali and Beyer

(1979), the induction of oestrous behaviour, including the standing reflex, is regulated by a number of factors. Neuroendocrine mechanisms within the central nervous system mediate the sexual receptivity or lordosis in females. A certain threshold level of oestrogen is needed to induce the oestrous behaviour, but there is considerable individual variation within the same breed in the amount of oestrogen required for induction. The integrity of the ventral hypothalamus is essential for the display of oestrous behaviour for all species. The preoptic area of the brain could, however, have an inhibitory effect on the oestrous behaviour.

In the present investigation, the weaning season did not influence many of the oestrous symptoms. A slight decrease in the duration of pro-oestrus was seen during seasons with long photo periods compared to the season with short and increasing day length (paper IV). No other significant differences in the duration and intensity of the oestrous symptoms could be seen in the present investigation (paper IV). Other studies have, however, suggested that the duration of standing oestrus can be prolonged by long photo periods (Signoret, 1967; Perera and Hacker, 1984).

Relationships between some of the oestrous symptoms at puberty and after the first weaning have been found (paper V). Among pigs not showing standing reflex at puberty, 21.4% ovulated within 10 days of weaning without showing a detectable standing reflex (paper V). The corresponding result among pigs showing standing reflex at puberty was 6.2%. In addition, the heritability has been estimated to be 0.29 for the ability to show standing reflex at puberty (Rydhmer et al., 1994). Pigs not showing standing reflex at ovulation are recorded in practice as having a high age at puberty or a long interval from weaning to oestrus. No relationship was seen between the duration of the standing oestrus at puberty and after weaning (paper V). The heritability for the duration of the standing oestrus at puberty has been shown to be 0.16, which is the lowest heritability value of all the oestrous symptoms (Rydhmer et al., 1994). This low heritability is partly due to a very small variation in the duration of the standing oestrus. The total duration of the vulvar symptoms at puberty has the highest heritability (0.38) of all oestrous symptoms (Rydhmer et al., 1994). There are relationships between the duration and intensity of the vulvar symptoms at puberty and after the first weaning (paper V). A gilt showing long and strong vulvar symptoms is more likely to also show long and strong vulvar symptoms after the first weaning, compared to gilts showing short and weak vulvar symptoms at puberty.

For practical use it is important to remember that selection for distinct and strong oestrous symptoms at puberty could improve the oestrous symptoms also after the first weaning. A problem gilt, when it comes to oestrous symptoms seems to be more likely than the average gilt to also become a problem sow. A fairly high frequency of the primiparous sows does not show any pro-oestrus at the first oestrus after weaning. Sows with a longer IWO (within the range 3-6 or 3-9 days) may have a shorter standing oestrus and a shorter interval from the beginning of standing reflex to ovulation than sows with a shorter IWO. For this reason there is

a greater risk of inseminating sows with a longer IWO too late, which results in lower farrowing rates and smaller subsequent litter size, than sows with a shorter IWO. Careful oestrous detection by persons with good knowledge of oestrous symptoms can reduce the number of sows not detected in oestrus, although the sows have normal to weak oestrous symptoms.

Factors influencing the variation in weight loss between sows during lactation

Many studies have shown that nutrition during lactation (feeding, energy and protein levels) has a great influence on the body reserves, live weight and backfat thickness in sows. Primiparous sows usually lose more weight during lactation than older sows. They have high energy and protein requirements, not only for milk production but also for growth to mature weight. In practice, the same feeding regime is often used for all sows in a herd, although a more individually based feeding level could be beneficial for the constitution and body reserves of the sow, as discussed by Neil (1996). Very few investigations, however, have studied the variation in weight loss during lactation in sows kept under the same feeding regime. The present investigation shows that there is a large variation in weight loss during lactation, although the sows have been fed according to the same feeding regime, based on litter size (paper I). When analysing sows nursing an equal number of piglets, the variation in weight loss is still very large (paper I). In addition, the heritability for body weight loss during the first lactation has been shown to be fairly large (0.4) (Rydhmer et al., 1992). In the present investigations a lactation period of six weeks was used. Most of the weight loss during lactation occurred during the first two weeks, while very little weight was lost during the fifth and sixth week of lactation (Sterning, unpublished).

A good appetite is important during lactation. The voluntary feed intake increases until the 6th parity (O'Grady et al., 1985), with the largest increase from the first to the second parity (Young et al., 1990). The energy and protein requirements for primiparous sows during lactation may therefore exceed even the voluntary feed intake. Individual differences in appetite are probably responsible for some of the variation in weight loss during lactation. It is well known that overfeeding during gestation results in a reduced feed intake during lactation, compared to restricted feeding during gestation. Selection for increased leanness in pigs could also have an unfavourable effect on the voluntary feed intake, depending on the methods used (Riley, 1989). In sows showing very large weight loss during lactation, the frequency of sows with reduced appetite on the day of weaning was higher than in sows losing less weight (paper II). The appetite may have been reduced for some time but, unfortunately, this was not recorded. A short period with lack of appetite was also more common among sows with large weight loss during lactation than among sows with small weight loss (paper II). There is strong positive correlation between litter size, litter weight gain and body weight loss of the sow (Danielsen and Nielsen, 1982). A large litter requires a very large daily feed intake of the sow. Reducing very large first litters could therefore be favourable for the sow's ability

to consume sufficient amounts of feed for milk production and for the sow's own growth to mature weight.

Individual differences in the regulation of the energy metabolism during lactation (Rojkittikhun et al., 1992) may be responsible for a part of the variation in weight loss. This information must be considered in future studies on the effect of nutrition and body reserves on the interval from weaning to oestrus.

Health during lactation may influence the variation in weight loss during lactation. Sows showing large relative weight loss during lactation (RWL III) had a higher total disease incidence during lactation than sows with small or medium weight loss (RWL I-II) (paper II). The incidence of different kinds of disease also differed. Mastitis was the most common disease among class III sows, whereas farrowing disorders, including manually assisted farrowing and problems with milk let-down, were the most common diseases among class I sows (showing small relative weight loss). Thus, it appears that good health during lactation may reduce the weight loss during lactation among sows kept under the same restricted feeding regime based on litter size. Although there were differences in the total disease incidence during lactation, sows showing large weight loss during lactation did not have a higher frequency of infections or injuries at weaning than sows showing small weight loss (paper II). Results of analysis of a blood sample drawn during late lactation indicated no differences in the incidence of sub-clinical infections between sows showing large or small weight loss, respectively, during lactation (paper II). With a lactation length of six weeks the sows appeared to have recovered from the infections and injuries incurred during early lactation.

Conclusions

The following conclusions were drawn from the present investigations on primiparous sows kept under the same restricted feeding regime during lactation, based on litter size:

- Without boar stimulation daily after weaning, 60 per cent of the sows showed standing reflex and ovulated within 10 days of weaning (SO), whereas almost 12 per cent ovulated without showing standing reflex (O). By using boar stimulation, the percentage of SO sows increased remarkably (87%) and the percentage of O sows decreased (2%). In the part of the investigation where boar stimulation was used the average body weight loss during lactation was a few kilograms less than in the part where boar stimulation was not used. This fact also contributed to the difference in the percentage of SO sows.

- When boar stimulation was not used after weaning and 60 percent of the sows returned to oestrus within 10 days of weaning there was a significantly higher body weight and backfat loss among sows neither showing standing reflex nor ovulating within 10 days of weaning (NSO) than among SO sows. This difference was not evident when boar stimulation was used and a higher percentage of the sows returned to oestrus within 10 days. Among SO sows, boar-stimulated or not, there was a significant positive correlation between the interval from weaning to oestrus (IWO) and both body weight loss during lactation and litter weight gain. Sows weaned during the season with short and increasing day length, boar-stimulated or not, had the highest frequency of SO sows.

- Sows showing large weight loss during lactation had a higher total disease incidence during lactation than sows with small weight loss. The kinds of disease also differed, mastitis being the most common disease among sows showing large weight loss whereas farrowing disorders were the most common among sows showing small weight loss. Very few differences were seen in the clinical health at weaning between sows showing large or small weight loss, respectively. However, a higher percentage of sows showing large weight loss had reduced appetite on the day of weaning and low condition scores than sows showing small weight loss. Sub-clinical infections during late lactation, as indicated by blood parameters, did not seem to be more common among sows showing large weight loss than among sows showing small weight loss during lactation.

- No significant difference in the total disease incidence or in the different kinds of diseases during lactation was seen between NSO and SO sows, although mastitis seemed to be more common among NSO sows. In addition, very few differences in the clinical health at weaning were seen between NSO and SO sows, but NSO sows seemed to have a higher frequency of low condition scores than the SO sows.

- Sows showing large weight loss during lactation seemed to be in a more catabolic state during late lactation than sows showing small weight loss, as indicated by blood parameters. There were, however, no significant differences in the metabolic state between NSO and SO sows in late lactation.

- The duration of pro-oestrus and the total duration and intensity of the vulvar symptoms increased from the first to the second oestrus after weaning. The duration of the standing oestrus did not differ between the first and second oestrus. Fairly high repeatability values were seen between the pro-oestrus period and the intensity of the vulvar symptoms at the first and at the second oestrus after weaning.

- Few factors influenced the duration and intensity of the oestrous symptoms. The duration of pro-oestrus increased with an increasing IWO, and was significantly longer in the season with short and increasing day length compared to seasons with long day length. The frequency of sows with no pro-oestrous symptoms increased with increasing litter size. The total duration and the intensity of the vulvar symptoms were unfavourably influenced by a large litter. The duration of standing oestrus decreased with an increasing IWO (within the range 3-9 days).

- Pigs younger at puberty had a shorter IWO compared to pigs older at puberty. This relationship could also be seen in both phenotypic and genetic correlations between age at puberty and IWO. The risk of not showing standing reflex at the first ovulation after weaning was higher among pigs not showing standing reflex at puberty compared to pigs showing standing reflex at puberty.

- There was a significant positive correlation between the total duration of the vulvar symptoms at puberty and after weaning. A higher frequency of pigs with strong vulvar symptoms at puberty also had strong vulvar symptoms after weaning compared to pigs with no or weak vulvar symptoms at puberty.

Acknowledgements

The studies presented in this thesis were performed at the Department of Obstetrics and Gynaecology, in co-operation with the Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences, Uppsala, Sweden. The work was supported by founds from The Farmers' Research Council for Information and Development.

First of all I wish to thank the pigs, and especially the primiparous sows, for being such interesting and wonderful animals. Thanks to them I feel that this work has been worth all the efforts.

I also wish to express my gratitude to the following:

Professor Stig Einarsson, Head of the Department of Obstetrics and Gynaecology and my major supervisor, who in some way made me go for the Ph.D., although that was the last thing I wanted when I started working at OG. I very much appreciate his support, unfailing interest, encouragement and constructive criticism.

Dr. Kjell Andersson, Head of the pig division at the Department of Animal Breeding and Genetics, and my assistant supervisor, who guided me into the world pig production and statistical analyses. I am very grateful for his support and interest.

Lena Eliasson-Selling and Lotta Rydhmer, my co-workers, for their encouraging interest and enthusiasm on pig reproduction.

Nils Lundeheim, for always having some time for my statistical problems and for his kind support and interest.

Colleagues in the pig group at OG for providing a stimulating scientific atmosphere and for their support and interest. Special thanks to Fredrik Hultén for helping me during my maternity leaves.

Ulrica Bexelius, Susanne Hägg Eriksson, Carina Fors, Carola Jansson and Rigmor Shamar, five very important persons, for their superb technical assistance. They always managed to keep an inspiring and friendly atmosphere, although the sows, boars and jugular veins did not always cooperate.

Per-Erik (Pekka) Nyström, Eva Ringmar-Cederberg and Susanne Stern, for very good co-operation and for always showing an interest in my work.

The staff of the stable, Ulf Hermansson, Eva Norling, Ulla Schmidt and all the others who worked their for a short time, for taking such good care of the animals. I am also very grateful for your kind interest and for the help with oestrous detection during weekends and with blood sampling.

Birgitta Berner and Anita Liljeholm, for always providing me with secretarial help when I needed. Special thanks to Anita for helping me with the final preparation of the thesis.

Ove Larfors and the computer group at Funbo-Lövsta, for always managing to help me with my computer problems, although they were very busy with other things.

All the staff at OG and at the research station Funbo-Lövsta, for their help and for providing a stimulating and friendly atmosphere. Friday coffee brakes were something special not only in a scientifical meaning. Special thanks to Ann-Britt Andersson, Anna Israelsson and Anita Jansson, for their kind interest.

The Department of Clinical Chemistry, for analysing all the blood samples. Special thanks to Henrik Holst, for helping me to understand the results of the blood analyses in paper II.

Yvonne Tizard, for always providing me with her expert linguistic revision.

Johnny Carlsson, for excellent library service.

Carlotte Lindqvist, one of my very best friends, for making this thesis a little personal, after all.

My parents, Ingrid and Erik, and my sister Annica, for their never failing interest and support, although they had some difficulties to understand my choice of occupation. Without the help of my parents, during the last months, this thesis would never have been ready in time.

Anneli and Mikael, my children, for being the joy of my life, and keeping me in touch with reality.

Tom, my companion in life, not for helping me but, nevertheless, for being an important and beloved part of my life.

References

Aherne, F.X., and R.N. Kirkwood, 1985. Nutrition and sow prolificacy. J. Reprod. Fert. Suppl. **33**, 169-183.

Andersson, A.-M., S. Einarsson, L.-E. Edqvist, and N. Lundeheim, 1984. Endocrine pattern and external oestrous symptoms at second and fourth oestrus in gilts. Anim. Reprod. Sci. **6**, 301-310.

Andersson, H., M. Forsberg, K. Lundström, and L. Rydhmer, 1996. The influence of long-day and short-day photoperiods on pubertal timing and boar taint in the domestic pig. In: Proceedings of the 13th International Congress on Animal Reproduction, Sydney, Australia. Abstract P 16-16.

Armstrong, J.D., and J.H. Britt, 1987. Nutritionally-induced anestrus in gilts: metabolic and endocrine changes associated with cessation and resumption of estrous cycles. J. Anim. Sci. **65**, 508-523.

Aumaitre, A.J., C. Legault, J. Dagorn, and M. LeDenmat, 1976. Influence of farm management and breed type on sows conception-weaning interval and productivity in France. Livest. Prod. Sci. **3**, 78-83.

Benjaminsen, E., and K. Karlberg, 1981. Postweaning oestrus and luteal function in primiparous and pluriparous sows. Res. Vet. Sci. **30**, 318-322.

Bidanel, J.P., J. Gruand, and C. Legault, 1996. Genetic variability of age and weight at puberty, ovulation rate and embryo survival in gilts and relations with production traits. Genet. Sel. Evol. **28**, 103-115.

Booth, P.J., 1990. Metabolic influences on hypothalamic-pituitary-ovarian function in the pig. In: DJA Cole, GR Foxcroft and BJ Weir (Ed.) Control of Pig Reproduction III. J. Reprod. Fert. Suppl. **40**, 89-100.

Booth, W.D., and B.A. Baldwin, 1983. Canges in oestrous cyclicity following olfactorial bulbectomy in post-pubertal pigs. J. Reprod. Fert. **67**, 143-150.

Bosu, W. T. K., L.-E. Edqvist, P. Lindberg, K. Martinsson, and E.D.B. Johansson, 1976. The effect of various dosages of lynestrenol on plasma levels of oestrogen and progesterone during the menstrual cycle in rhesus monkey. Contraception **13**, 677-684.

Brooks, P.H., and D.J.A. Cole, 1970. The effect of the presence of boar on the attainment of puberty in gilts. J. Reprod. Fert. **23**, 435.440.

Burger, J.F., 1952. Sex physiology of pigs. Onderspoort J. Vet. Res. Suppl. **2**, 3-218.

Cole, D.J.A., M.A. Varley, and P.E. Hughes, 1975. Studies in sow reproduction. 2. The effect of lactation length on the subsequent reproductive performance of the sow. Anim. Prod. **20**, 401-406.

Dalin, A.-M., T. Nanda, F. Hultén, and S. Einarsson, 1995. Ovarian activity at naturally attained oestrus in the sow. An ultrasonographic and LH study. Acta vet. scand. **36**, 377-382.

Danielsen, V., and H.E. Nielsen, 1982. Søer vægt ændringer i relation til kuldnummer, race og kuldstørrelse. Statens Husdyrbrugsforsøg, June Number 415.

Dewey, C.E., S.W. Martin, R.M. Friendship, and M.R. Wilson, 1994. The effects on litter size of previous lactation length and previous weaning-to-conception interval in Ontario swine. Prev. Vet. Med. **18**, 213-223.

Duncombe, W.G., 1964. The colorimetric determination of nonesterified fatty acids in plasma. Clin. Chem. Acta **9**, 122-125.

Dyck, G.W., 1988. The effect of housing facilities and boar exposure after weaning on the incidence of postlactational anoestrus in primiparous sows. Can. J. Anim. Sci. **68**, 983-985.

Ehnvall, R., Å. Blomqvist, S. Einarsson, and K. Karlberg, 1981. Culling of gilts with special references to reproductive failure. Nord. Vet.-Med. **33**, 167-171.

Einarsson, S., and I. Settergren, 1974. Fertility and culling in some pig breeding herds in Sweden. Nord. Vet.-Med. **11**, 427-442.

Einarsson, S., C. Linde, and I. Settergren, 1974. Studies of the genital organs of gilts culled for anoestrus. Theriogenology **2**, 109-113.

Eisenweiner, H.G., 1976. Kinetische Bestimmung des Harnstoffes mit dem LKB-system. J. Clin. Chem. Clin. Biochem. **14**, 261-264.

Eliasson L., 1989. A study on puberty and oestrus in gilts. J. Vet. Med. A **36**, 46-54.

Eliasson, L., 1991. Relationships between puberty and production traits in the gilt. 2. Oestrous symptoms at puberty. Anim. Reprod. Sci. **25**, 255-264.

Fabiny, D. L., and G. Ertinghausen, 1971. Automated reaction rate method for determination of serum creatinine with the Centri Chem. Clin. Chem. **17**, 696-700.

Fahmy, M.H., 1981. Factors influencing the weaning to oestrus interval in swine: A review. World Rev. Anim. Prod. **17**, 2, 15-28.

Foxcroft, G.R., J.R. Cosgrove, and F.X. Aherne, 1996. Relationship between metabolism and reproduction. In: Proceedings of the 14th International Pig Veterinary Society Congress, Bologna, Italy, pp 6-9.

Hemsworth, P.H., and G.J. Coleman, 1996. Human-animal relationship and productivity in pigs. In: Proceedings of the 14th International Pig Veterinary Society Congress, Bologna, Italy, pp 3-5.

Holder, R.B., R.O. Bates, and W.R. Lamberson, 1993. Effect of decreased age at puberty on lifetime productivity of sows. In: Proceedings of the 4th International Conference on Pig Reproduction, Missouri-Columbia, USA. Paper 86.

Hultén, F., T. Segall, and A. Persson, 1991. Misstänkt proliferativ hemmorrhagisk enteropati (PHE) i en svensk svinbesättning. Svensk Veterinär tidning **43**, 395-401.

Hultén, F., B.R. Zhang, M. Forsberg and A.-M. Dalin, 1995. Applying a progesterone assay to faecal samples collected from sows during the oestrous cycle. Reprod. Dom. Anim. **30**, 101-105.

Hurtgen, J.P., A.D. Leman, and B. Crabo, 1980. Seasonal influence on oestrous activity in sows and gilts. J. Am. Vet. Med. Assoc. **176**, 119-123.

Johansson, K., 1992. Programs for single and multiple trait analysis with derivative free REML. User's notes. Swedish University of Agricultural Sciences, Uppsala, Sweden.

Karlberg K, 1980. Factors affecting postweaning oestrus in the sow. Nord. Vet.-Med. **32**, 185-193.

Karlbom, I., 1982. Attainment of puberty in female pigs: Influence of boar stimulation. Anim. Reprod. Sci. **4**, 313-319.

Kemp, B., and N.M. Soede, 1996. Relatioship of weaning-to-estrus interval to timing of ovulation and fertilization in sows. J. Anim. Sci. **74**, 944-949.

King, G.J., 1978. Occurrence of postweaning oestrus in primiparous and pluriparous sows. In: Proceedings of the 5th International Pig Veterinary Society Congress, Zagreb. Paper K. A. 12.

King, R.H., and A.C. Dunkin, 1986. The effect of nutrition on reproductive performance of first litter sows. 4. The relative effects of energy and protein intakes during lactation on performance of sows and their piglets. Anim. Prod. **43**, 319-325.

Koketso, Y., G.D. Dial, J.E. Pettigrew, W.E. Marsh, and V.L. King, 1996. Influence of imposed feed intake patterns during lactation on reproductive performance and on circulating levels of glucose, insulin, and luteinizing hormone in primiparous sows. J. Anim. Sci. **74**, 1036-1046.

Kunavongkrit, A., S. Einarsson, and I. Settergren, 1982. Follicular development in primiparous lactating sows. Anim. Reprod. Sci. **5**, 47-56.

Love, R.J., 1981. Seasonal infertility in pigs. Vet. Rec. **109**, 407-409.

Love, R.J., G. Evans, and C. Kluiec, 1993. Seasonal effects on fertility in gilts and sows. J. Reprod. Fert. Suppl. **48**, 191-206.

Mauget, R., 1982. Seasonality of reproduction in the wild boar. In: D. J. A. Cole and G. R. Foxcroft (Editors), Control of Pig Reproduction. Butterworths Scientific, London. pp. 509-526.

Mburu, J.N., S. Einarsson, A.-M. Dalin, and H. Rodriguez-Martinez, 1995. Ovulation as determined by transrectal ultrsonography in muktiparous sows: Relationships with oestrous symptoms and hormonal profiles. J. Vet. Med. A. **42**, 285-292.

Megraw, E.M., D.E. Dunn, and H.G. Biggs, 1979. Manual and continousflow colorimetry of triacylglycerols by a fully enzymatic method. Clin. Chem. **25**, 273-278.

Merks, J.W.M., and R.J.F. Molendijk, 1995. Genetic correlations between production traits and first parity traits. In: Proceedings of the 46th Annual Meeting of the

European Association for Animal Production, Prague, Czech Republic. Abstract P 4.11.

Morali, G., and C. Beyer, 1979. Neuroendocrine control of mammalian oestrous behaviour. In: C. Beyer (Editor), Endocrine Control of Sexual Behaviour. Raven Press, New York, pp. 33-75.

Mullan B.P., and I.H. Williams, 1990. The chemical composition of sows during their first lactation. Anim. Prod. **51**, 375-387.

Neil, M., 1996. Effects of ad libitum feeding in lactation and the timing of its introduction on sow performance. Doctoral Thesis. Dep. of Animal Nutrition and Management, Swedish University of Agricultural Sciences, Uppsala, Sweden. Report 237.

Nogueira, L.A.G., Silva Filho, J.M., Marcatti Neto, A., Silva, M.I.F. and Bergmann, J.A.G., 1984. Heat occurence and length in gilts and sows.In: Proceedings of the 8th International Pig Veterinary Society Congress, Ghent, Belgium. Paper 302.

O'Grady, J.F., P.B. Lynch, and P.A. Kearney, 1985. Voluntary feed intake by lactating sows. Livest. Prod. Sci. **12**, 355-365.

Ozasa, H., and K.G. Gould, 1982. Demonstration and characterisation of estrogen receptor in chimpanzee sex skin: correlation between nuclear receptor levels and degree of swelling. Endocrinology **111**, 125-131.

Paterson, A.M., and G.P. Pearce, 1990. Attainment of puberty in domestic gilts reared under long-day or short-day artificial light regimens. Anim. Reprod. Sci. **23**, 135-144.

Pearce, G.P., and A.N. Pearce, 1992. Contact with a sow in oestrus or a mature boar stimulates the onset of oestrus in weaned sows. Vet. Rec. **130**, 5-9.

Perera, A.N.M., and R.R. Hacker, 1984. The effects of different photoperiods on reproduction in the sow. J. Anim. Sci. **58**, 1418-1422.

Persson, A., A.E. Pedersen, L. Göransson, and W. Kuhl, 1989. A long term study on the health status and performance of sows on different feed allowances during late pregnancy. Acta vet. scand. **30**, 9-17.

Prunier A., J.Y. Dourmand, and M. Etienne, 1994. Effect of light regimen under various ambient temperatures on sow and their litter performance. J. Anim. Sci. **72**, 1461-1466.

Prunier, A., H. Quesnel, M. Messias de Braganca, and A.Y. Kermabon, 1995. Environmental and seasonal influences on the return-to-oestrus after weaning in primiparous sows. In: Proceedings of 46th Annual Meeting of the European Association for Animal Production, Prague, Czech Republic. Abstract P 4.7.

Reese, D.E., B.D. Moser, E.R. Peo Jr, A.J. Lewis, D.R. Zimmerman, J.E. Kinder, and W.W. Stroup, 1982. Influence of energy intake during lactation on the interval from weaning to first estrus in sows. J. Anim. Sci. **55**, 590-598.

Reese, D.E., E.R. Peo Jr, and A.J. Lewis, 1984. Relationship of lactation energy intake and occurrence of postweaning estrus to body and backfat composition in sows. J. Anim. Sci. **58**, 1236-1244.

Riley, J.E., 1989. Recent trends in pig production: the importance of intake. In: The Voluntary Food Intake of Pigs (ed. J.M. Forbes, M.A. Varley, and T.L.J. Lawrence). British Society of Animal Production. Occasional Publication no. 13, pp. 1-5.

Rojanasthien, S., S. Einarsson, and I. Settergren, 1987. Follicular development in lactating, postweaning and anoestrus primiparous sows. Acta vet. scand. **28**, 421-427.

Rojkittikhun, T., Einarsson, S. and Edqvist, L.-E., 1993a. Pattern of plasma oestradiol-17β in relation to the interval from weaning to oestrus in sows. Acta vet. scand. **34**, 95-97.

Rojkittikhun, T., S. Einarsson, L.-E. Edqvist, K. Uvnäs-Moberg, and N. Lundeheim, 1992. Relationship between lactation-associated body weight loss, levels of metabolic and reproductive hormones and weaning-to-oestrous interval in primiparous sows. J. Vet. Med. A **39**, 426-432.

Rojkittikhun, T., S. Einarsson, K. Uvnäs-Moberg, and L.-E. Edqvist, 1993b. Body weight loss during lactation in relation to energy and protein metabolism in standard-fed primiparous sows. J. Vet. Med. A **40**, 249-257.

Rydhmer, L., L. Eliasson-Selling, K. Johansson, S. Stern, and K. Andersson, 1994. A genetic study of estrous symptoms at puberty and their relationships to growth and leanness in gilts. J. Anim. Sci. **72**, 1964-1970.

Rydhmer, L., K. Johansson, S. Stern, and L. Eliasson-Selling, 1992. A genetic study of pubertal age, litter traits, weight loss during lactation and relations to growth and leanness in gilts. Acta Agric. Scand., Sect. A, Anim. Sci. **42**, 211-219.

Schenk, P.M., 1967. An investigation into the oestrus symptoms and behaviour of sows. Z. Tierzücht. Züchtbiol. **83**, 87-110.

Signoret, J. P., 1967. Durée du cycle oestrien et de l'oestrus chez la truie. Action du benzoate d'oestradiol chez la femelle ovariectomisée. Ann. Biol. Anim. Bioch. Biophys. **4**, 407-421.

Signoret, J.P., 1970. Reproductive behaviour of pigs. J. Reprod. Fert. Suppl. **11**, 105-117.

Simonsson, A., 1988. Näringsrekommendationer och fodermedelstabeller till svin. Konsulentavdelningen, Report No. 66. Swedish University of Agricultural Sciences, Uppsala, Sweden, 61 pp.

Soede, N.M., J.P.T.M. Noorhuizen, and B. Kemp, 1992. The duration of ovulation in pigs studied by transrectal ultrasonography is not related to early embryonic diversity. Theriogenology **38**, 653-666.

Stanchev, P., A. Kunavongkrit, L.-E. Edqvist, and H. Eriksson, 1984. Receptors for estrogens and progesterone in porcine cervix. Theriogenology **21**, 757-766.

Stanchev, P., H. Rodriguez-Martinez, L.-E. Edqvist, and H. Eriksson, 1985. Oestradiol and progesterone receptors in the pig oviduct during the oestrous cycle. J. Steroid Biochem. **22**, 115-120.

Stanchev, P., H. Rodriguez-Martinez, L.-E. Edqvist, and H. Eriksson, 1990. Characterization of uterine sex steroid receptors in pig and their variation during the oestrous cycle. J. Steroid Biochem. **35**, 689-699.

Statistical Analysis System (SAS) Institute Inc., 1985, 1987. SAS User's Guide. Statistic version 5, 6. SAS Institute, Cary, NC.

Stern, S., K. Johansson, L. Rydhmer, and K. Andersson, 1993. Performance testing of pigs for lean tissue growth rate in a selection experiment with low and high protein diets. 1. Experimental design and efficiency of selection. Acta Agric. Scand., Sect. A, Anim. Sci. **43**, 136-143.

Stern, S., N. Lundeheim, and K. Andersson, 1995. Performance and carcass traits after five generations of selection for lean tissue growth rate in pigs. Anim. Sci. **61**, 341-346.

Sterning, M., and N. Lundeheim, 1995. Some factors influencing pregnancy rate and subsequent litter size in primiparous sows. Acta vet. scand. **36**, 353-365.

Stork, M.G., 1979. Seasonal reproductive inefficiency in large pig breeding units in Britain. Vet. Rec. **104**, 49-52.

Ten Napel, J., A.G. De Vries, G.A.J. Buiting, P. Luiting, J.W.M. Merks, and E.W. Brascamp, 1995. Genetics of the interval from weaning to oestrus in first-litter sows: Distribution of data, direct response of selection, and heritability. J. Anim. Sci. **73**, 2193-2203.

Vesseur P.C., and B. Kemp, 1993. Importance of the weaning to oestrus interval for sow performance and identification of underlying factors. In: Proceedings of the 4th International Conference on Pig Reproduction, Missouri, USA. Abstract 102.

Whittemore, C.T., and H. Yang, 1989. Physical and chemical composition of the body of breeding sows with differing body subcutaneous fat depth at parturition, differing differing nutrition during lactation and differing litter size. Anim. Prod. **48**, 203-212.

Xue, J.L., G.D. Dial, W.E. Marsh, P.R. Davies, and H.W. Momont, 1993. Influence of lactation length on sow productivity. Livest. Prod. Sci. **34**, 253-265.

Xue, J.L., G.D. Dial, W.E. Marsh, and P.R. Davies, 1994. Multiple manifestations of season on reproductive performance of commercial swine. J. Am. Vet. Med. Assoc. **204**, 1486-1489.

Young, L.G., G.J. King, J.S. Walton, I. McMillan, M. Klevorick, and J. Shaw, 1990. Gestation energy and reproduction in sows over four parities. Can. J. Anim. Sci. **70**, 493-506.

Personal communication

Vet. Arne Persson, Department of Obstetrics and Gynaecology, Swedish University of Agricultural Sciences, Box 7039, S-750 07 Uppsala, Sweden.

Acta Universitatis Agriculturae Sueciae
presents doctoral theses from the faculty of agriculture, landscape architecture and horticulture, the faculty of forestry and the faculty of veterinary medicine at the Swedish University of Agricultural Sciences. Each faculty has its own subseries, Agraria, Silvestria and Veterinaria, respectively, with separate numbering.

ISSN 1401-6257
ISBN 91-576-5229-5