

University of Helsinki, Finland
Faculty of Veterinary Medicine
Department of Clinical Veterinary Sciences
and
Swedish University of Agricultural Sciences,
Department of Animal Environment and Health



Behaviour and physiology of lactating sows - associations with piglet performance and sow postweaning reproductive success

By
Anna Valros

Academic dissertation

To be presented with the permission of the Faculty of Veterinary Medicine, University of Helsinki, for public criticism in Auditorium Maximum, Hämeentie 57, Helsinki on March 28th, 2003 at 12 noon

Helsinki 2003

Supervised by: Professor Bo Algers
Department of Animal Environment and Health
Swedish University of Agricultural Sciences, Sweden

Professor Hannu Saloniemi
Department of Clinical Veterinary Sciences
University of Helsinki, Finland

Associate professor Margareta Rundgren
Department of Animal Nutrition and Management
Swedish University of Agricultural Sciences, Sweden

PhD Marek Špinka
Ethology Group
Research Institute of Animal Production, Czech Republic

Reviewed by: Associate professor Dan Weary
Faculty of Agricultural Sciences
The University of British Columbia, Canada

PhD Beat Wechsler
Centre for proper housing of ruminants and pigs
Swiss Federal Veterinary Office, Switzerland

Opponent: Professor Per Jensen
Department of Biology, IFM
Linköping University, Sweden



Yliopistopaino
Helsinki 2003
ISBN 952-91-5676-6 (nid.)
ISBN 952-10-0991-8 (PDF)

CONTENTS

Abstract	5
List of original articles	9
1. Introduction: Piglet production – past, present and future	10
1.1 Pig production in Finland.....	10
1.2 Problems facing the piglet production unit.....	10
1.3 Piglet production and welfare	11
1.4 Sow maternal abilities and the future.....	12
2. Survey of the literature	14
2.1 Causes of piglet mortality.....	14
2.2 Natural maternal behaviour of the sow.....	15
2.2.1 Nursing behaviour.....	15
2.2.2 Weaning.....	17
2.3 Maternal physiology of the sow.....	17
2.3.1 Changes in metabolic rate from prepartum to weaning.....	17
2.3.2 Maternal endocrinology of the sow.....	19
2.4 Reproduction-inhibiting effect of lactation.....	22
2.4.1 Resource use for milk production and effects on subsequent reproductive success.....	22
2.4.2 Suckling stimuli inhibit reproductive functions.....	22
2.5 Is it possible to increase piglet performance by selecting for good mothers?..	24
2.6 Summary of literature review.....	25
3. Aims	27
3.1 General aim.....	27
3.2 Specific hypotheses.....	28
4. Material and methods	30
4.1 Animals, housing and management.....	30
4.2 Behavioural measurements (I-III, V).....	32
4.3 Surgery and care of catheter (II-V).....	33
4.4 Blood sampling (II-V).....	33
4.5 Hormone and metabolite analyses (II-V).....	35
4.6 Oestrus detection and ultrasonographic examination (IV-V).....	35
4.7 Determination of ovulation rate (IV-V).....	36
4.8 Variables.....	36
4.9 Statistical analyses.....	37
4.10 Missing data.....	38
5. Results	40
5.1 Litter statistics.....	40
5.2 Pattern of nursing behaviour.....	40
5.3 Changes in metabolite and hormone concentrations and sow weight loss.....	42
5.4 Different measures of the metabolic state.....	42
5.5 Metabolic state of the sow and nursing behaviour.....	43
5.6 Effects of nursing behaviour on average piglet weight gain.....	45

5.7 Effect of metabolic state of the sow on piglet and litter weight gain.....	45
5.8 Differences in weight loss, metabolite and hormonal concentrations, and nursing behaviour between sows with low or high mortality.....	45
5.9 Nursing-induced changes in lactation-related hormones on day 14.....	46
5.10 Hormonal concentrations and the sows' use of resources for milk output.....	50
5.11 Oxytocin and prolactin concentrations and the sows' piglet-directed behaviour.....	50
5.12 Differences in reproductive functions between sows with high and low catabolic rates during lactation.....	51
5.13 Differences in reproductive functions between sows with differing nursing behaviour.....	52
6. Discussion.....	53
6.1 Methodological considerations.....	53
6.2 Patterns of nursing behaviour.....	55
6.3 Physiological changes in the sow during lactation.....	56
6.4 Sow metabolism and piglet growth and survival.....	57
6.5 Associations between sow behaviour and metabolism.....	58
6.6 Associations between nursing behaviour and piglet weight gain.....	59
6.7 Oxytocin, prolactin, somatostatin and milk production.....	60
6.8 Oxytocin, prolactin and maternal behaviour.....	62
6.9 Metabolic status during lactation and postweaning reproductive success.....	62
6.10 Nursing behaviour and postweaning reproductive success.....	63
7. Conclusions.....	64
Acknowledgements.....	66
References.....	70
Papers I-V.....	80



Abstract

Piglet mortality occurs at an ethically and economically unacceptable level in modern pig production, and efforts should be focused on reducing the problem. A considerable part of the mortality is directly or indirectly related to the maternal abilities of sows; starvation, crushing and a combination of these are accepted as the most common causes of mortality in live-born piglets during the lactation period. The farrowing crate was developed to reduce mortality by crushing, but it has been criticized for reducing the welfare of sows. An increase in production unit size has followed from the increasing economic pressure on the pig industry. Simultaneously, consumers have become increasingly aware of animal welfare issues, and alternative production systems, such as organic farming, have become increasingly popular. These two developments both increase the importance of good maternal abilities of sows; in large, intensive units the opportunities for individual care of sows and piglets during and after farrowing are limited. On the other hand, in more extensive systems where sows are kept unrestrained or in groups, the sow has increased opportunities to perform natural maternal behaviour, but if she lacks the ability, the system does not compensate for this. So far there has been no direct breeding for maternal abilities, but this possibility should be investigated. Since the profit of a piglet-producing unit to a great extent is determined by the number of piglets produced per year per sow, it is also important to consider fertility aspects.

The maternal ability of a sow forms through complex interactions between an array of various behavioural and physiological characteristics. The sow should behave in a way optimising milk intake by her litter. She should be efficient at using available energy for milk production, and since the feed intake of lactating sows usually fails to meet the demands for milk production, this means lactating sows need to switch to a catabolic state and use their body reserves for milk production. Furthermore, milk production and maternal behaviour are both largely under endocrine control. To enable selection for

sows with good maternal abilities, it is important to understand the underlying mechanisms and to find phenotypic measures for these. On the other hand, a high level of energy deficiency in the sow and abundant suckling stimuli provided by the piglets can inhibit reproductive functions. Therefore, associations between behaviour and physiology during lactation and postweaning reproductive success should also be investigated.

To investigate the traits that characterise sows with good maternal abilities and if these traits are associated with postweaning reproductive success, 21 multiparous sows were followed intensively during a 5-week lactation and after weaning. No experimental manipulations of sows or litters were performed, since the aim was to study undisturbed behaviour and physiology of individual sows. The sows were housed in individual pens both during and after lactation and were not restrained at any point. Piglet weight gain and survival were used as measures of sow lactational performance. The piglets were weighed individually on the day after farrowing, on days 4, 8, 15 and 22 postpartum, and at weaning. The sows were weighed on the day after farrowing, on days 15 and 22 postpartum and at weaning. On day 2 after the 2nd postweaning oestrus, the sows were slaughtered and their genital tracts removed for examination.

Sow behaviour was recorded during 5 days of lactation (days 3, 6, 13, 20 and 30). The behavioural variables included different aspects of nursing behaviour as well as piglet-directed behaviour. A jugular catheter was used to minimise disturbance of sows during blood samplings. The metabolic state of the sows was studied intensively on days 7 and 21 of lactation and described in terms of sow weight change, metabolite (glucose, urea and non-esterified fatty acid (NEFA)) and hormonal (insulin) concentrations. Also the prolactin concentration was sampled on days 7 and 21 postpartum. In addition, the sows were sampled for NEFA from day 14 postpartum onwards. Lactation-related endocrinology was studied on day 14 postpartum. During and between 3 successful nursings, the sows were sampled frequently for analyses of oxytocin, prolactin and somatostatin. Reproductive endocrinology was measured daily from day 14 postpartum onwards (progesterone) and on days 14 and 21 of lactation (luteinizing hormone (LH) and oestradiol-17 β (E₂)). Postweaning reproductive success was estimated as interval from weaning to the 1st and to the 2nd oestrus, as oestrus to ovulation interval and as ovulation rate.

The nursing behaviour of the sows changed during lactation in a manner indicating the presence of an ongoing weaning process, starting already dur-

ing the 1st week postpartum. Nursing duration decreased, the sows terminated larger proportions of nursings and spent larger proportions of time lying on the udder, thus avoiding udder stimulation by the piglets. Most aspects of nursing behaviour showed high repeatability within sow between days, indicating that the various aspects of nursing behaviour are individually stable characteristics, at least within one lactation. All measures of the metabolic state used indicated that the sows were more catabolic on day 21 than on day 7 postpartum: the NEFA and urea concentrations were higher, while the glucose and insulin concentrations were lower on the latter day. The sows also showed a higher daily weight loss during week 3 than during the first 2 weeks of lactation. Since milk production usually peaks during the 3rd week of lactation, the negative energy balance was probably due to a high demand for milk production at this time. Even though the sows in this study were fed near-to *ad libitum* levels, they appeared unable to compensate for this by feed intake. Nursing behaviour and the metabolic state of sows appeared to be linked via associations with insulin and prolactin.

Several aspects of sow characteristics were related to piglet performance. A high successful nursing frequency throughout lactation appeared to be associated with high piglet weight gain also in a situation where sow nursing behaviour was not experimentally altered. The same connection has been reported in studies of a more experimental nature. Sows that were efficient at switching to a high catabolic state (measured as a high plasma NEFA concentration) early in lactation had lower piglet mortality. Oxytocin appeared to be more important for milk production than simply functioning as a trigger for milk ejections. The oxytocin concentration between nursings was positively correlated with high piglet growth and the oxytocin concentration during nursings was positively correlated with high NEFA concentration and large weight loss by the sow.

This study did not report any apparent conflicts between physiology and behaviour that would favour piglet performance on one hand and postweaning reproductive success on the other. Even though the sows differed in their metabolic state during lactation and this difference was evident also after weaning, a high catabolic state was not associated to an inhibited postweaning reproductive success. It is possible that sows fed at a near-to *ad libitum* level do not reach an energy balance negative enough to have detrimental effects on fertility. High nursing frequency, which appeared to be the most important factor associated with piglet growth, did not associate negatively with repro-

ductive functions, but a long duration of udder stimulus (i.e. nursing duration) was associated with an inhibited reproductive endocrinology.

This study, even though it is descriptive in nature and does not explain causal relationships, indicates that high successful nursing frequency, high catabolic state early in lactation and high oxytocin level are all associated with increased piglet performance. Behaviour, metabolism and endocrinology of lactating sows are all interrelated. Neither a high level of fat metabolism (measured as NEFA) nor a high nursing frequency was related to inhibited reproductive functions. Instead, sows with long duration of udder massage had inhibited reproductive endocrinology.



List of original articles

This thesis is based on the following original articles, referred to in the text by their Roman numerals:

I) A.E. Valros, M. Rundgren, M. Špinka, H. Saloniemi, L. Rydhmer, B. Algers, 2002. Nursing behaviour of sows during 5 weeks lactation and effects on piglet growth. *Appl. Anim. Behav. Sci.* 76, 93-104.

II) A. Valros, M. Rundgren, M. Špinka, H. Saloniemi, L. Rydhmer, F. Hultén, K. Uvnäs-Moberg, M. Tománek, P. Krejčí and B. Algers, 2003. Metabolic state of the sow, nursing behaviour and milk production. *Livest. Prod. Sci.* 79, 155-167.

III) A. Valros, M. Rundgren, M. Špinka, H. Saloniemi, F. Hultén, K. Uvnäs-Moberg, M. Tománek, P. Krejčí and B. Algers, 200X. Oxytocin, prolactin and somatostatin in lactating sows: associations with mobilisation of body resources and maternal behaviour. Submitted

IV) F. Hultén, A. Valros, M. Rundgren, S. Einarsson, 2002. Reproductive endocrinology and postweaning performance in the multiparous sow Part 1. Influence of metabolic status during lactation. *Theriogenology* 58, 1503-1517.

V) F. Hultén, A. Valros, M. Rundgren, S. Einarsson, 2002. Reproductive endocrinology and postweaning performance in the multiparous sow Part 2. Influence of nursing behaviour. *Theriogenology* 58, 1519-1530.



1. Introduction: Piglet production – past, present and future

The pig was first domesticated about 9000 years ago and has always been used mainly for its meat and skin. Pig production was at an early stage conducted in two different manners, either intensively or extensively. This resulted in two distinct types of pigs: large, light-coloured and almost hairless pigs for indoor breeding and smaller, more agile, hairy and dark pigs for outdoor rearing. The pig has generally been considered a poor man's animal, because it can be fed with household waste (for a review on pig domestication see Clutton-Brock, 1999).

1.1 Pig production in Finland

The pork industry is an important part of Finnish farm animal production, with about 1.3 million pigs and over 180 000 sows in 2000 (Finnish Ministry for Agriculture and Forestry). Lately the industry has been going through extensive changes because of huge economic pressure, especially since Finland joined the EU. This can be seen as a decrease in number of production units, accompanied by larger unit sizes (Sternberg, 2002). Even so, piglet production in Finland has traditionally been small-scaled, and still is, with an average unit size of 62 sows (Maaseutukeskusten liitto, 1999). The most common size of a piglet production unit still varies between 30 and 45 sows (Sternberg, 2002).

1.2 Problems facing the piglet production unit

Piglet production units are faced with several serious problems, influencing both financial results and animal welfare. Since the financial results are mainly dependent on the number of piglets weaned per sow and year, the two most important factors affecting the economic result negatively are sow fertility problems and piglet losses (Sternberg, 2002). The more piglets weaned per

sow and year, the higher are the economic benefits (Maaseutukeskusten liitto, Sikataloustarkkailu, 2000). The total preweaning piglet mortality (including stillbirths) on Finnish farms averages over 20%, but there is huge between-farm variation (Sternberg, 2002), indicating that environmental and husbandry aspects play an important role. Finnish sow units usually have individual farrowing pens, either with or without crates.

Several of the health problems facing farrowing sows are apparently related to piglet performance. Leg problems are one of the most common reasons for culling sows (13.7% in 2001) (Sternberg, 2002), and can also affect piglet survival since poor leg and muscle condition probably increase piglet mortality. Dry sows housed in stalls have been reported to have higher perinatal mortality rates than loose-housed sows with more opportunity for exercise during gestation (Billie et al., 1974). Leg problems can probably also increase piglet mortality due to crushing, because sow muscle control is important for controlled lying-down (Marchant and Broom, 1996). Among the health problems commonly treated in Finnish sow herds, mastitis-metritis-agalactia (MMA) is the most frequently occurring: 15.4% of all veterinary treatments recorded in the national health-recording scheme were due to MMA in 2001. Problems at farrowing are also rather common, accounting for 10.7% of all treatments. On the 942 farms included in the health-recording scheme, 2768 cases of treatment for farrowing difficulties and udder diseases were recorded in 2001 (Rautala, 2002). Algers and De Passillé (1991) suggested that improvement in sow health and milk production is of great importance in reducing piglet mortality.

1.3 Piglet production and welfare

Consumer awareness of farm animal welfare has increased during the recent decades, with general opinion reflected in both legislation and consumer choices. For example, in a guidebook for farm buildings from as late as 1987 (Nurmisto, 1987), it is explicitly stated that the sow's area should be restricted by the use of a farrowing crate. On the other hand, the new national Animal Welfare legislation that was adopted in 1997 recommends that sows should be able to turn around in their farrowing pens (decision nr 13/EEO/1997). The newly adopted changes in the EU pig directive (91/630/ETY) also improve pig welfare, e.g. by making the provision of nest material to sows in late gestation obligatory. In some countries, e.g. Sweden and Switzerland (transition

period until 2007), the use of farrowing crates is already prohibited by law.

Consumer choices are reflected in an increased demand for ecologically produced meat and for meat from production systems with high welfare standards. There has been a rapid increase in organic farming in Finland, even though organic pig farming is still rather marginal. In 2001 there were 24 farms in Finland producing organic pork meat, of which approximately half also produced piglets (Peltomäki, 2002, *personal communication*).

A high mortality rate in farmed animals is always related to poor welfare, and piglet mortality is no exception. Therefore, piglet survival should be improved not only for financial reasons, but also to improve the welfare of animals on pig farms and the public image of the industry. The farrowing crate was developed to reduce piglet mortality and make management procedures easier (Clough, 1984; Algiers and De Passillé, 1991). On the other hand, the farrowing crate greatly restricts sow movements. During pre-farrowing and farrowing the sow goes through an array of hormonal changes inducing behaviours related to nest building and farrowing. The lack of opportunity to act on these internally triggered behavioural needs probably has disadvantageous effects on the sow's welfare (for a review, see Clough, 1984), and can be seen as increased levels of stress-related hormones (cortisol and adrenocorticotrophic hormone (ACTH)) (Lawrence et al., 1994; Jarvis et al., 1997). In addition, the farrowing crate has negative effects on sow health; incidences of both MMA and farrowing difficulties have been reported to be higher in crated sows than in sows housed loosely in pens (Bäckström, 1973). These, in turn, can increase piglet mortality (Bäckström et al., 1984). Recent studies have reported longer farrowing duration in crates compared with systems allowing more freedom of movement, especially in gilts (e.g. Klocek et al., 2000; Thodberg et al., 2002). On the other hand, other studies have failed to find such effects (e.g. Lawrence et al., 1995; Fraser et al., 1997).

1.4 Sow maternal abilities and the future

Sow maternal abilities play a very important role for piglet survival and growth, and increasing focus should be placed on the ability of sows to care for their offspring. In the future this will become even more important because of two totally opposite developments in the pig industry. Firstly, increasing unit size and more intensified production makes individual care of farrowing and newly farrowed sows more difficult, since more animals are looked after

by each caretaker. As human intervention decreases, it becomes increasingly important that sows have good maternal abilities. Secondly, extensive production systems, in which sows are kept loosely in pens or even outdoors, demand the usage and functioning of the actual mother-young interaction. As the environment becomes less restrictive, the sows can perform more of their natural maternal behaviour, but if they have impaired maternal abilities, the production environment does not compensate for this.



2. Survey of the literature

2.1 Causes of piglet mortality

Piglet mortality rates vary between studies, housing systems and countries, but in most cases the reported value lies between 10% and 20% (e.g. Glastonbury; Edwards et al., 1986; Dyck and Swierstra, 1987; Edwards et al., 1994). In Finland, total piglet mortality averaged 22.4% in 2001 (mortality of live-born 13.9%) on 764 farms included in the National Litter Recording Scheme (Sternberg, 2002). It is generally accepted that stillbirths (or perinatal deaths), starvation and crushing by the sow are the most common causes of mortality in preweaning piglets (Glastonbury, 1977; Edwards et al., 1986; Dyck and Swierstra, 1987; Edwards et al., 1994). It is often difficult to accurately define the factors leading to deaths of piglets, and it has been stated that e.g. the role of crushing is overestimated (Algers and De Passillé, 1991). Piglets that are hungry tend to spend more time close to the sow's udder, thus probably seeking warmth and trying to stimulate milk production. These weak piglets become crushed more easily, and death is therefore often caused by a combination of starvation and trauma caused by the sow (Weary et al., 1996). Algers and De Passillé (1991) estimated that starvation is the primary or ultimate cause for piglet deaths in as many as 50% of the cases.

Mortality is highest during the 1st days after farrowing; approximately 75% of the mortality has been reported to occur during the 1st week of lactation (Glastonbury, 1976; Edwards et al., 1986). The causes of mortality differ at different stages of the pre-weaning period. Physical factors, such as suffocation during parturition and trauma are commonly involved in mortality of piglets during the first 4 days, as is starvation and septicaemia, while various viral and bacterial infections are important causes of mortality later in lactation (Glastonbury, 1977).

2.2 Natural maternal behaviour of the sow

The maternal behaviour of the sow is unique, since many aspects of this are generally common in predators but not in hoofed animals. Firstly, the sow isolates herself from the group and builds an elaborate nest. Secondly, the sow gives birth to a litter, while most other hoofed animals only give birth to one or two offspring at a time (Clutton-Brock, 1999). For the sow to successfully bring up a large litter without compromising future reproductive success, her behaviour and physiology must have been modified accordingly during evolution.

2.2.1 Nursing behaviour

Every sibling in a litter will fight for its own survival, while the sow benefits from raising as many piglets as possible. Much of the suckling behaviour of piglets can be viewed as a way to communicate individual nutritional needs of the piglet (Algers, 1993), whereas sow nursing behaviour can be viewed as a means of ensuring an even distribution of milk to all the piglets (Fraser, 1980). The sow has no milk cistern where milk can be stored, but milk is let down directly from the alveoli at each nursing, and a pig cannot compensate for one missed nursing by attempting to suckle individually (Fraser, 1980). Milk is only let down during one short milk ejection (lasting approx. 10-20 s) at synchronised nursings, when the majority of the litter is present and stimulating the udder (Fraser, 1980; Ellendorff et al., 1982). Milk ejection never occurs in the absence of udder stimulation (Ellendorff et al., 1982) and the need for a long duration of massage to stimulate milk letdown increases with decreasing number of piglets present (Algers et al., 1990). Competition between littermates is further reduced by the establishment of a teat order (Ellendorff et al., 1982).

Nursing behaviour in the pig is fairly stereotypic (Ellendorff and Poulain, 1984). Nursings can either be initiated by the sow by calling the litter or by piglets squealing by the sow's head or stimulating the udder (Ellendorff et al., 1982). During the 1st week of lactation, the sow initiates the majority of nursings, but this rate declines with proceeding lactation (Jensen, 1988; Bøe, 1993; Illmann and Madlafousek, 1995). The sound of other sows and piglets nursing often stimulates nursing behaviour and sows tend to synchronise their nursing behaviour (Wechsler and Brodmann, 1996), probably to reduce cross-suckling, i.e. piglets sucking sows other than their own dam.

The first phase of a nursing begins after the sow has lain down on her side, exposing her udder. The litter then starts massaging the udder vigorously and the grunting of the sow becomes rhythmic, the grunting rate being slightly less than one grunt per second (Ellendorff et al., 1982). This phase is referred to as the premassage and lasts for 1 to 3 min (Ellendorff et al., 1982; Algers et al., 1990; Algers et al., 1991). The grunting rate of the sow then increases and this causes the piglets to turn from massaging to sucking the teat (Algers and Jensen, 1985). Before milk ejection occurs there is a nonnutritive slow-sucking phase when the piglets suck on their teats with 1-2 mouth movements per second (Rushen and Fraser, 1989). When the grunting rate of the sow peaks at almost 2 grunts per second (Ellendorff et al., 1982), the piglets switch to a fast-sucking phase, showing 4-5 mouth movements per second. It is during this phase, which lasts for 10 to 30 s (Fraser, 1980) that milk ejection occurs (Rushen and Fraser, 1989).

After the milk ejection, the piglets again begin massaging and nosing the udder and this postmassage phase can last from less than a minute to several minutes (Ellendorff et al., 1982). The total nursing period has been reported to last an average of about 6 min, the range being from less than 2 min to 16 min (Ellendorff et al., 1982; Algers et al., 1991) and longer early in lactation (Watson and Bertram, 1980). The interval between milk ejection is approximately 45 to 55 min (Fraser, 1977; Ellendorff et al., 1982) and increases as lactation proceeds (Watson and Bertram, 1980; Algers et al., 1990; Illmann and Madlafousek, 1995). The nursing interval has been observed to be longer in a seminatural setting than in sows kept indoors (Castrén et al., 1989) and to be affected by the presence of other sows. Watson and Bertram (1980) found longer mean intervals between successful nursings in solitary housed and unrestrained sows (mean 52.2 min) than in sows crated in a shed with other sows (mean 46.4 min).

Nursings can either be interrupted by the sow (by standing up or rolling over on the sternum) or by the piglets walking away or falling asleep at the udder. In free-ranging sows over two-thirds of the observed sucklings during the first 3 days postpartum were ended by the piglets falling asleep at the udder (Castrén et al., 1989). As lactation proceeds, increasing numbers of nursings are terminated by the sow (Watson and Bertram, 1980; Jensen, 1988).

Different aspects of sow nursing behaviour, such as nursing frequency (Špinková et al., 1997, Auld et al., 2000) and massage time (Algers and

Jensen, 1991) have been suggested to influence piglet performance.

2.2.2 Weaning

The weaning process in the pig is gradual and under natural conditions piglets are weaned as late as 14-17 weeks after birth (Jensen, 1986; Jensen and Recen, 1989). The length of the lactation period is dependent on the nutritional state of the sow and the amount of food available in the environment (Jensen and Recen, 1989). The weaning process seldom includes aggressive behaviour (Jensen, 1986), instead the sow alters her nursing behaviour to make it more and more costly for the piglets to nurse (Jensen and Recen, 1989). The intervals between nursing increase, the sow allows shorter massaging of the udder and increasing numbers of nursings occur while the sow is standing (Jensen, 1988; Jensen and Recen, 1989; Bøe, 1991). When the sow has the opportunity to walk away from her litter, she can avoid their attention by doing so, and sows do spend an increasing amount of time away from their litter with proceeding lactation when kept outdoors (Jensen, 1988) or in get-away pens (Bøe, 1991). In a farrowing pen or crate, this is not the case and the sow must avoid nursing attempts and massaging of the udder by other means, such as lying on her belly.

2.3 Maternal physiology of the sow

2.3.1 Changes in metabolic rate from prepartum to weaning

During gestation, the dam builds up her body reserves to provide for milk production after parturition. After parturition there is a switch from an anabolic to a catabolic state, giving the mammary gland metabolic priority over other tissues (Collier et al., 1984), seen for example as a lower activity of lipoprotein lipase and rate of fatty acid synthesis (Flint et al., 1979). Even though lactating sows are often fed *ad libitum*, the feed intake cannot fully compensate for milk production and the energetic balance of sows is usually negative throughout lactation. To meet the energetic requirements of milk production, sows mobilise body reserves (for a review see Quesnel and Prunier, 1995).

The level of the catabolic state during lactation is dependent on feeding level and milk output, but there is also individual variation (Rojkittikhun et al., 1993b). Results on the direction of metabolic changes with proceeding lactation are so far inconsistent. The peak milk yield in sows has been found to oc-

cur at approximately 2-3 weeks postpartum (Armstrong et al., 1986; Rojkittikhun et al., 1993a; Toner et al., 1996) and is associated with lower blood glucose levels, because a maximum amount of glucose is used for milk production at this time (Rojkittikhun et al., 1993a). The high demand for energy has been reported to cause higher levels of catabolism in the sow during week 3 than earlier in lactation (Rojkittikhun et al., 1993a; Kraetzl et al., 1998). Hultén et al. (1993), on the other hand, found a peak in sow weight loss and catabolism during the 1st week of lactation. The metabolic rate is usually estimated by sow weight loss, body fat loss and by sampling for metabolic hormones and metabolites such as glucose, urea and non-esterified fatty acid (NEFA).

Glucose

During lactation, plasma glucose levels are generally low, as a consequence of high mammary utilisation (for a review see Quesnel and Prunier, 1995). About 50% of the blood glucose is used for milk production (Spincer et al., 1969). The glucose level is strongly influenced by feeding, the levels rising significantly during the 1st hour after feeding (De Braganca and Prunier, 1999). Prefeeding glucose levels have been found to rise in the 1st week of lactation and decline in the 3rd and 4th weeks, being lowest in high litter-gain sows (Kraetzl et al., 1998). Rojkittikhun et al. (1993a) failed to find a correlation between prefeeding glucose levels and weight loss in the sow, and could therefore not connect glucose directly to the usage of body reserves for milk production by the sow. This is not surprising, since sows are usually fed diets high in starch and therefore do not run short of glucose (Kraetzl et al., 1998).

Urea

Urea is a by-product of protein metabolism, and high urea levels could indicate a high level of muscle mass usage (Kraetzl et al., 1998). Kraetzl et al. (1998) also found that urea concentrations change at feeding and are dependent on the amount of food consumed. Since these authors did not find evidence for high protein mobilisation during lactation in standard-fed sows, they proposed that the high mobilisation of body fat (indicated by a rise in NEFA) during lactation produces sufficient energy for the mammary gland, even without high protein mobilisation. Results on changes in urea concentration during lactation are inconsistent and are not directly connected with sow

weight loss (Hultén et al., 1993; Rojkittikhun et al., 1993a; Le Cozler et al., 1998).

NEFA

NEFA is a product of fat metabolism, and is a reliable sign of the presence of a catabolic state, since only a small amount is derived from feed intake. Instead, NEFA levels decline after meals (De Braganca and Prunier, 1999), rising again after a couple of hours. NEFA levels have been reported to rise at the end of gestation and be highest during mid- and late lactation, the level being highest in sows with high weight-gain litters (Kraetzel et al., 1998), although results are contradictory (Hultén et al., 1993; Rojkittikhun et al., 1993b; Le Cozler et al., 1998). Since the level of NEFA is a reflection of fat metabolism it is dependent on sow back-fat thickness and feeding level (Baidoo et al., 1992a; Hultén et al., 1993). The NEFA concentration is commonly used as a measure of postpartum energy status (Kraetzel et al., 1998) and fat catabolism of sows (Armstrong et al., 1986; Hultén et al., 1993).

2.3.2 Maternal endocrinology of the sow

Both maternal behaviour and metabolism are known to be at least partly under endocrinological control. For example, sow nest-building prior to farrowing has been found to be induced by an increase in prolactin concentration. Furthermore, a rise in oxytocin has been recorded at the end of the nest-building phase (Widowski, 1990; Castrén et al., 1994). The onset and maintenance of lactation are dependent on hormones such as prolactin (for a review see Farmer, 2001), while oxytocin is needed for the milk ejection reflex to occur (for a review see Goodman and Grosvenor, 1983). The maternal endocrinological state is also strongly influenced by stimuli from the litter (Algers et al., 1991; De Passillé et al., 1993; Špinka et al., 1999).

Oxytocin

Oxytocin is involved in several different aspects of maternal behaviour and physiology of mammals. In rodents, general maternal behaviour, such as pup grooming is induced by oxytocin (for a review see Argiolas and Gessa, 1991). In pigs oxytocin has not, to our knowledge, been directly connected with physical contact between sow and piglets as such, but is essential for the milk ejection reflex (Ellendorf et al., 1982; Algers et al., 1990). In addition, Algers et al. (1990) reported a correlation between the volume of nursing-related

grunting and amount of oxytocin released. Elevated concentrations of oxytocin are also involved in the termination of nest building and parturition in the sow (Castrén et al., 1993a, b).

The all-or-nothing function of oxytocin in triggering milk ejections is well known in pigs (for a review see Goodman and Grosvenor, 1983). Oxytocin concentrations rise rapidly during nursings, reaching peak levels just prior to milk ejection. This high-level oxytocin release during nursings normally only occurs if the litter provides enough udder stimulation (Algers et al., 1990) and is usually seen only in connection with nutritive nursings (i.e. nursings including milk ejection) (Rojkittikhun et al., 1993b). The amount of oxytocin released during the peak varies between sows and does not appear to be influenced by the number of piglets in the litter or the duration of udder massage (Algers et al., 1990). After milk ejections oxytocin concentrations again decline rapidly towards baseline levels (Ellendorff et al., 1982; Rojkittikhun et al., 1993b).

Oxytocin is also involved in the regulation of metabolism during lactation (Uvnäs-Moberg et al., 2001). In rats peripheral oxytocin has a positive effect on the release of insulin and glucagon and the level of glucose and thus probably increases the amount of glucose available for milk production (Björkstrand et al., 1996). Oxytocin has also been shown to influence the concentrations of serum NEFA in rats, the effect being dependent on the dose of oxytocin and the energetic state of the animal (Suva et al., 1980). It can thus be hypothesised that oxytocin is involved in the regulation of resource use for milk production.

Prolactin

Prolactin is one of the most important hormones involved in initiation and maintenance of milk production in mammals (Barber et al., 1992; Flint et al., 1995; Farmer et al., 1998). In addition, prolactin has been found to influence nursing behaviour and maternal responsiveness positively in rodents (Bridges et al., 1990; McCarthy et al., 1994). If prolactin release is inhibited during lactation, the maternal behaviour is severely disrupted, at least in the hamster (McCarthy et al., 1994).

In sows, prolactin levels begin to rise during the last week of gestation and maximum levels have been reported around parturition and during the first 2 weeks of lactation (Meunier-Salaun et al., 1991; Kraetzel et al., 1998). Prolactin is stimulated by udder massage (Algers et al., 1991; Rushen et al.,

1993; Špinka et al., 1999), but the increase is gradual and not sudden as is the increase in oxytocin. Prolactin reaches its highest concentrations 10-20 min after nursings (Einarsson et al., 1992; Rojkittikhun et al., 1993b; Špinka et al., 1999). The degree of nursing-induced increase in prolactin is influenced by massage duration and litter size (Mulloy and Malven, 1979; Dusza et al., 1981; Algers et al., 1991; de Passillé et al., 1993). Prolactin concentrations also increase after feeding (Armstrong et al., 1986).

As lactation proceeds the prolactin concentrations decline (Dubreuil et al., 1990), possibly as a result of lowered udder stimulation by the piglets (Armstrong et al., 1986). If lactation is interrupted by early weaning of the offspring, a rapid decrease in prolactin concentrations occurs (Dusza et al., 1981; Rojkittikhun et al., 1991).

Prolactin is also involved in regulation of the lactational metabolism; in rats a low insulin concentration during lactation allows prolactin to dominate the metabolism of adipose tissue (Flint et al., 1979). In addition, prolactin has been found to positively affect the amount of insulin receptors in the mammary gland (Flint, 1982; Baidoo et al., 1992) and can therefore be expected to function in determining maternal metabolic functions, possibly affecting the proportion of resource allocation for milk production.

Insulin

Insulin promotes the utilisation of glucose and amino acids by peripheral body tissues, which causes a decrease in nutrient use for milk production (Armstrong et al., 1986). The prefeeding insulin concentration increases from the day of parturition (De Passillé et al., 1993) and is food-dependent, being low before the morning feeding and then rising rapidly remaining at that level for several hours. The postfeeding rise in insulin vanishes after approximately 3 h (Le Cozler et al., 1998). The prefeeding insulin levels are elevated only during early lactation (Kraetzl et al., 1998), and the levels occurring later in lactation are lower than after weaning (Armstrong et al., 1986). The decrease towards peak lactation is probably a physiological response to the high utilisation of glucose for milk production (Rojkittikhun et al., 1993a). Insulin levels are higher in sows that lose less weight during lactation (Baidoo et al., 1992a; Rojkittikhun et al., 1993a). Therefore, high insulin concentrations during lactation probably indicate the presence of a low catabolic state.

Insulin has also been shown to influence milk production more directly. Flint et al. (1979) found that the number of insulin receptors in adipose tissue

as well as plasma insulin level in rats decreased after parturition, while insulin receptor numbers doubled in mammary tissue around parturition (Flint, 1985). The author suggested that this would decrease the rate of lipogenesis in adipose tissue, but enhance the sensitivity of the mammary tissue to insulin despite the decline in plasma insulin concentration.

Somatostatin

The gut hormone somatostatin has an inhibitory effect on digestive functions (Efendic and Uvnäs-Wallensten, 1983). Suckling normally causes a decline in somatostatin concentrations in sows, but the pattern is not consistent (Uvnäs-Moberg et al., 1984). The results are also variable in other species; e.g. breastfeeding in humans can either cause an increase or a decrease in concentration of somatostatin, although concentrations are always lower 1 h after breastfeeding compared with basal levels (Widström et al., 1988). Some degree of association between nursing stimuli and somatostatin appears to exist, since Algiers et al. (1991) found a negative correlation between somatostatin concentration and duration of premassage in pigs. The inhibitory effect of suckling on somatostatin possibly allows for increased digestive functions during lactation.

2.4 Reproduction-inhibiting effect of lactation

2.4.1 Resource use for milk production and effects on subsequent reproductive success

Nutritional deficiencies during lactation affect several reproductive functions negatively: the gonadotropin-releasing hormone (GnRH) pulse generator is inhibited, gonadotropin release is decreased (Armstrong and Britt, 1987), follicle development is impaired (Quesnel et al 1998a, b) the weaning-to-service interval increases (King and Williams, 1984; Zak et al., 1998) and ovulation rate is possibly impaired (Zak et al., 1997). If high milk production and thus efficient piglet growth causes a negative energy balance in the sow, this can be expected to impair future reproductive functions. There are, however, large variations in reproductive performance between sows, even when fed similarly during lactation (Sterning et al., 1990; Rojkittikhun et al., 1992).

2.4.2 Suckling stimuli inhibit reproductive functions

The reproductive performance of sows is not only affected by the nutritional

status of the sow. The stimulus provided by nursing piglets is considered to be the most important factor inhibiting ovarian activity during lactation (Stevenson et al., 1981; De Rensis et al., 1993), but this effect does not appear to be mediated by negative effects of the milk-related hormones prolactin or oxytocin (Rojkhittikhun, 1992). The activity of the hypothalamus-pituitary-ovarian (HPO) axis increases with proceeding lactation, possibly as a result of decreasing nursing frequency (Stevenson and Britt, 1980; Stevansson et al., 1981). There is normally an immediate increase in activity of the HPO axis at weaning, leading to ovulation (Rojkhittikhun et al., 1992; Quesnel et al., 1998b). The amount of udder stimulus provided by the piglets is determined by several aspects of behaviour: in addition to nursing frequency, the nursing duration and allowance of massage by the sow are also important.

Luteinizing hormone (LH)

LH stimulates several reproductive functions: it increases maturation of the follicles and stimulates oestrogen secretion, ovulation and the formation of corpora lutea (and thus secretion of progesterone). LH secretion is stimulated by GnRH, which in turn is regulated by neural input (such as from the suckling stimulus) and oestrogen levels (Eckert et al., 1988). The inhibition of LH is one of the principal causes of lactational anoestrus (for a review see Varley et al., 1989). As lactation proceeds, the level and pulse frequency of LH increase (Baidoo et al., 1992a; Rojkittikhun et al., 1993b), possibly as a result of reduced inhibitory stimuli from udder massage. Rojkittikhun et al. (1993b) found a negative, although non-significant correlation between number of sucklings and LH pulses on day 20 of lactation.

Oestradiol -17 β

Oestradiol -17 β (E_2) is the most potent of the oestrogens and is secreted from the ovarian follicles and corpora lutea. E_2 is stimulated by LH and follicle-stimulating hormone (FSH) and regulates reproductive cycles, e.g. oocyte maturation (Eckert et al., 1988). E_2 concentrations have been found to decrease after parturition, increasing again around peak lactation (week 3 post-partum; Varley et al. (1989)). After weaning, there is a significant increase in E_2 (Rojkittikhun et al., 1992).

Progesterone

Progesterone originates from the corpora lutea and is important in preparing

the uterus for pregnancy and maintaining pregnancy. Progesterone secretion during the luteal phase is stimulated by high levels of LH (Eckert et al., 1988). The progesterone level decreases before parturition, but remains at a slightly higher level for least 3 days after farrowing (Ash and Heap, 1975; Kunavongkrit, 1984; Meunier-Salaun et al., 1991; De Passillé et al., 1993). The decreasing progesterone concentrations cause the inhibition of milk synthesis to cease and are thus important for the initiation of lactation (Eckert et al., 1988). Lowering of the progesterone level is important for lactational metabolism; it has been shown in rats that progesterone increases adipose lipid storage as well as number of insulin receptors in adipose tissue (Flint, 1985), thus decreasing the energy metabolism for milk production. In pigs, high early postpartum levels of progesterone have been found to correlate negatively with litter weight gain (De Passillé et al., 1993).

2.5 Is it possible to increase piglet performance by selecting for good mothers?

So far, there has been minimal direct breeding for maternal characteristics in sows. It is known that certain behavioural traits related to maternal abilities are heritable, such as aggressiveness towards piglets (Van der Steen et al., 1988). Recent field studies, performed as questionnaires posted to farmers, also indicate that maternal reactivity is a heritable trait (Vangen, et al., 2002). Since the number of piglets weaned has been included in the breeding goals, some indirect selection for maternal abilities has inevitably been done, but this is in systems manipulated by humans, e.g. by aiding during parturition and by mixing litters. On the other hand, selection for large litters has increased piglet mortality (Johnson et. al., 1999). To also promote the individual sow's maternal abilities in the absence of humans, the focus may need to be rethought. Selection for increased piglet survival as a direct effect has been shown to be successful. Survival is genetically correlated with a decrease in within-litter variation in birth weight and possibly also with a decrease in birth weight (Knol, 2001).

Verheijen (2001) studied sows with differing estimated breeding values for mothering ability (defined as potential of a sow to raise live-born piglets entrusted to her) and showed that selection for mothering ability can improve piglet survival, without negative effects on other litter features. Selection for mothering ability reduces the interval to first colostrum intake of piglets, pos-

sibly because sows may spend more time in a lying position during and after farrowing, they may attract piglets to the udder more efficiently (e.g. stronger odour of the udder) and they may give milk more readily than sows with low mothering abilities. Physiological factors may also affect mothering ability: sows with high breeding values for mothering ability have lower glucose tolerance during late gestation. This means there is a longer period of free glucose in the blood, increasing both energetic gain of foetuses and milk production potential, since glucose is the primary precursor for lactose (Verheijen, 2001)

Other common breeding goals, such as selection for lean growth, can have adverse effects on piglet survival. McKay (1993) found a negative genetic correlation between lean gain and piglet survival and stated that the increase in mortality rate was mainly due to sow traits. But it is also possible that piglets may have lower maturity at birth, and thus lower survival rates, after selection for increased lean gain (Herpin et al., 1993). This is supported by the finding of Kerr and Cameron (1996) that in lines selected for high food conversion to lean growth or low daily food intake, litter size was smaller and piglet birth weight lower compared with their control lines.

2.6 Summary of literature review

The most common causes of mortality are starvation and crushing by the sow. Therefore, it can be concluded that the sow plays an important role in determining the survival rate of the litter. It is known that sows differ in milk production capacity and that the survival rate varies greatly between litters. Milk output is determined both by physiological and behavioural characteristics of the sow. The endocrinological state of the lactating sow needs to favour both resource use for milk production and stimulate maternal behaviour. To produce milk, sows must be efficient at allocating energy into milk production. Since feeding usually does not compensate for this energy usage, the lactating sow commonly enters a catabolic state. Finally, for the milk to reach the piglets, the sow needs to behave in a way that favours efficient transfer of nourishment to the piglets.

The performance of a sow is usually defined as the total number of piglets weaned per year. This number is influenced not only by the litter size, but also by the postweaning reproductive success. Since both energy deficiency and high level of nursing stimulation are known to inhibit reproductive functions, it is possible that sows with high-performing litters show decreased

postweaning reproductive success.

Some positive evidence for improving the maternal abilities of sows by selecting directly for maternal ability has been presented, although it is not known in detail which are the specific maternal characteristics influencing litter performance.



3. Aims

3.1 General aim

The primary aim of this thesis was to investigate which behavioural and physiological traits of a sow influence the performance of her piglets. Piglet growth and mortality are used as measures of piglet performance. Piglet growth is important per se, since an even, rapid growth of the litter is favourable, but also because there is a positive association between piglet survival and litter growth. Secondly, the aim was to study sow reproductive performance in a broader sense i.e. to determine whether sow investment in the present litter influences her investment in future reproduction. The focus was set on maternal characteristics of individual sows, to determine whether sows differ in aspects of maternal ability and if these differences are individually repeatable within one lactation. Fulfilling these two basic assumptions is the first step in investigating opportunities for breeding for maternal ability.

Although other authors have addressed similar problems, most previous studies of interaction between sow characteristics and piglet performance have included experimental procedures, such as manipulated nursing intervals (Špinková et al., 1997) or cross-suckling of litters (Auld et al., 2000). In order to obtain different metabolic states, feeding manipulations have often been used (e.g. Armstrong et al., 1986; Kirkwood et al., 1993). Although the use of experimental manipulations allow for clearer conclusions about causal relationships, the results might not be applicable for sows under normal conditions. In addition, manipulations such as restrictive feeding, might cause the animals stress, and therefore interfere with milk production or reproductive performance (Rivier et al., 1991; Tsuma et al., 1996). Thus, since we desired to obtain information on an individual basis and in a situation as close to normal piglet production as possible, we did no experimental manipulations of the animals and sows were disturbed as little as possible.

To our knowledge, the relationship between sow behaviour and physiology, piglet performance and sow reproductive functions has not yet been described under such conditions and during the full course of lactation. Much happens during a 5-week lactation: piglets grow, develop and become increasingly independent. Thus also the demand for maternal investment changes over the course of lactation. In order to understand the relationships between maternal investment, piglet performance and sow reproductive success, it is also important to describe how sow behaviour and physiology changes during lactation

3.2 Specific hypotheses

1. Sow nursing-related behavioural changes with proceeding lactation and certain aspects of an ongoing weaning process can already be seen during the first weeks of lactation: nursing frequency and nursing duration decreases and the sow performs increasing amounts of massage-avoiding behaviour, such as lying on the belly.
2. Nursing behaviour is not merely a randomly influenced characteristic, but individual sows differ in their behaviour and the behaviour shows repeatability from day to day.
3. The demand for mobilisation of body resources by the sow for milk production increases with proceeding lactation (from weeks 1 to 3 postpartum), a fact that should be reflected in the metabolic state of the sow.
4. Behaviour favouring efficient transfer of nutrients (e.g. high nursing frequency and allowance for increased udder stimulation) is associated with the presence of a high catabolic state, possibly via hormones, such as prolactin and insulin.
5. Individual differences in sow nursing behaviour are reflected in piglet growth: high piglet growth is achieved with frequent milk ejections and the allowance for increased udder stimulation.
6. Individual differences in the capability of similarly fed sows to use body reserves for milk production are reflected in piglet growth and survival: effi-

cient piglet growth and high survival are associated with the presence of a high catabolic state in the sow.

7. Milk production and maternal behaviour are largely under endocrine control. High levels of milk-related hormones such as prolactin and oxytocin enhance maternal characteristics, while anabolic hormones such as somatostatin inhibit digestive functions favouring milk production.

8. If investment in the present offspring is larger than the ingested energy, it will force the sow into an energetically negative state. Thus, catabolic rate during middle and late lactation is negatively related to postweaning performance.

9. Amount of udder stimuli provided by the piglets (measured as different aspects of nursing behaviour) is negatively related to the reproductive functions of the sow.



4. Material and methods

4.1 Animals, housing and management

Twenty-four pure-bred Yorkshire sows (3rd to 8th parity), originating from the Funbo-Lövsta experimental farm of the Swedish University of Agricultural Sciences (SLU) were used for the various studies. Prior to the observational period, the sows were group-housed during gestation (but individually fed) in a deep-litter system with approximately 16 sows per pen. The sows were studied in 6 batches of 4 animals each, during the time period July 1998 to June 1999. One week before expected farrowing the sows were catheterised. After one day of recovery they were moved to the experimental farrowing unit.

The experimental farrowing unit contained 6 individual pens in a temperature-regulated (15-20 °C) room (Figure 1). The pens were in 2 rows of 3



Figure 1. The experimental farrowing room, housing four sows at a time.



Figure 2. The experimental farrowing pen with the piglet creep area on the left-hand side of the picture.

pens each, separated by an aisle. Only the 4 corner pens were used for housing sows, leaving no possibility for physical contact between the sows. The pens measured 6.2 m² (295 x 210 cm) and a separate piglet creep area with a heat lamp was situated in one corner of the pen (Figure 2). Along the pen walls, steel pipes ran approximately 15 cm above the floor. The floor was covered with a rubber mat, except for a perforated steel-covered urine drainage area in the middle of the pen. The sows were kept loose during the entire lactation. After weaning the sows were kept in individual, straw-bedded pens in a room, where also an adult boar was housed.

Cleaning of the pens was conducted manually twice daily, in connection with feeding. The sows were given plenty of fresh straw after each cleaning to assure good coverage of the entire floor area. Around farrowing they were given an additional bale of straw in a rack. The noise level in the farrowing room was normally around 65 dB. Light was artificial at all times, the light regime being 14 h light:10 h dark (lights were on from 0700 to 2100). To make 24-h video-tapings possible a dim light was kept on during the night.

During lactation sows were fed sow feed with 12.4 MJ of metabolisable energy (ME)/kg and a lysine content of 6.9 g/kg. Rations were according to the Swedish norm (2.8 kg /day until the day after farrowing, when feed allowance was increased with 1 kg/day until the maximum amount was reached (2

kg + 0.6 kg/piglet)). From the day after weaning to the 1st oestrus the daily feed ration, given in 2 equal meals was 3.5 kg, and thereafter reduced to 3 kg/day (11.5 MJ ME/kg, 13% crude protein). Feeding was at 0730 and at 1530. Water was available on an *ad libitum* basis from a nipple. To insure adequate water intake during the lactation period the feed was mixed with water, and sows were given approximately 5 l of fresh water in a separate trough at each feeding. From day 22 postpartum piglets were given *ad libitum* access to creep feed. Water was available to the piglets on an *ad libitum* basis from nipples during the entire lactation.



Figure 3. Piglets were weighed individually on days 1, 4, 8, 15, and 22 after farrowing, and at weaning.

Piglets were marked individually with an ear tattoo on the day after farrowing (day 1 postpartum). The day during which farrowing commenced was labelled the farrowing day (day 0 postpartum) and was considered to end at 1800, later during lactation, the days were considered to start at 0700. The age of the piglets at the start of day 1 postpartum thus varied from 13 to 37 h. On day 4 postpartum all piglets were given 2 ml of ferrodextran (Pigeron vet[®]) i.m. to reduce the risk of anaemia, and male piglets were castrated. Neither tail-docking nor teeth-clipping was performed. Weaning occurred on day 35 ± 2 days postpartum. A macroscopic postmortem investigation was conducted on all piglets dying prior to weaning. Piglets were weighed individually on days 1, 4, 8, 15 and 22 postpartum and at weaning (Figure 3). The accuracy of the scale used for weighing the piglets was 0.1 g. Sows were weighed on days 1, 15 and 22 postpartum and at weaning. The sows were slaughtered with the use of a bolt gun 48 h after 2nd postweaning oestrus.

4.2 Behavioural measurements (I-III, V)

For behavioural observations sows and litters were videotaped for 24 h on

days 3, 6, 13, 20 and 30 postpartum, using video cameras attached to the ceiling directly above each pen. Recordings were made with time-lapse recorders (taking one frame per 0.18 s) in a 24-h mode and always started at 0830.

From these videotapes nursing behaviour and nasal contacts between sow and piglets were observed continuously, while the percentage of observations the sow spent in sternal recumbency was recorded by 5-min interval sampling. The starting time of each nursing was recorded, as well as its duration, terminator of the nursing and whether the nursing was successful or not. The sow was defined as terminator of the nursing when she either rolled over on her belly or stood up, thus preventing further udder massage by the piglets. Nursings were considered successful (i.e. including a milk-ejection) if a fast-sucking phase could be observed, i.e. if piglets were sucking intensively on the teats for about 15 s without interspersed teat massage or moving around (Watson and Bertram, 1980). A nursing was considered to have begun when more than half of the piglets were actively manipulating the udder and to have ended when more than half of the litter had left the udder or was inactive near the udder. Nursings were only recorded when the duration exceeded 60 s.

4.3 Surgery and care of catheter (II-V)

One week before expected farrowing the sows were surgically fitted with a permanent jugular vein catheter (Rodriguez and Kunavongkrit, 1983), to enable frequent blood sampling without disturbing the animals. General anaesthesia was induced by an initial injection of azaperon (Stresnil vet[®]) 40 mg/ml i.m., followed after about 30 min with a combination of tiletamin/zolazepam (Zoletil 100[®]) 100 mg/ml and romafidin (Sedivet vet[®]) 10 mg/ml i.m.. During the surgery general anaesthesia was maintained with halothane inhalation narcosis.

Throughout the study period the catheter was rinsed once daily with 5 ml of a NaCl (9 mg/ml)-solution containing 0.5% heparin (5000 IE/ml) and 1% Novocillin vet[®] (0.32 g/ml). During periods of frequent blood sampling, the catheter was rinsed with approximately 3 ml NaCl (9 mg/ml) solution containing 0.5% heparin (5000 IE/ml).

4.4 Blood sampling (II-V)

The catheters permitted blood sampling with minimal disturbance to the sows

and sows did not need to be restrained at any point for the blood sampling procedure (Figure 4). For the study of the metabolic state of the sows (II, III) blood samples were collected on days 7 and 21 postpartum. Samples were taken every hour on the hour for 16 h, beginning 30 min before morning feeding. In addition, when the sows were given feed (time 0) and began eating, samples were taken every 15 min for 1 h (i.e. at 0, 15, 30, 45 and 60 min). For the prolactin, insulin and somatostatin assays samples were collected in heparinised tubes, while samples used for the glucose assay were collected in tubes containing ethylenediaminetetraacetic acid (EDTA). For the NEFA and urea assays pure serum was collected.

On day 14 the sampling for the analyses of lactation-related hormones began between 1015 and 1130, depending on when a successful nursing first occurred. The first sample was taken approximately 15 min after the end of this nursing as a non-nursing sample. During the next three successful nursings, samples were withdrawn as fast as possible (interval approximately 30-120 s). The first sample was taken at the beginning of the pre-massage stage and the last during the post-massage stage, giving 2-5 samples per nursing. The variation in the interval between samples varied as the speed of the blood flow from the catheters varied both between and within sow, depending on the body posture. The difference in number of samples taken during each nursing depended on both the interval between samples and the duration of the nursing. If an unsuccessful nursing occurred, it was ignored and samples were instead collected during the following successful nursing. Three



Figure 4. Blood was sampled from a permanent catheter, fitted with a silicon tube to enable frequent blood sampling with minimal disturbance to the sow. Between samplings the tube was stored in a small bag between the shoulders of the sow.

additional non-nursing samples were taken: one sample 15 min after the end of each of the sampled nursings. Blood was collected in heparinised tubes containing 0.4 ml trasylol for assays of oxytocin and somatostatin and in heparinised tubes for the prolactin assay (III).

Reproductive endocrinology was studied intensively on days 14 and 21 postpartum and on the day after weaning (IV, V). Samples were drawn every 15 min from 0900 to 1500 and collected in heparinised tubes. LH analysis was performed on all samples while E_2 was assayed with 1 h intervals.

In addition, blood samples were collected in plain and heparinised tubes twice daily in connection with feeding (± 5 min) from day 14 of lactation until weaning, for analysis of NEFA (plain tubes) and progesterone (heparinised tubes). From the first day after weaning until 10 days after the first post-weaning oestrus samples for these analyses were drawn only in connection with morning feeding (IV, V).

4.5 Hormone and metabolite analyses (II-V)

Blood samples were analysed with various enzymatic methods for glucose, urea and NEFA (for further details on metabolite assays, see II, III and IV). Insulin was assayed using a double-antibody radioimmunoassay (RIA). Somatostatin RIA was performed according to Efendic et al. (1980). The plasma prolactin concentration was determined with double-antibody RIA essentially as described by Dusza and Krzymowska (1979) with some modifications, and oxytocin was assayed with RIA according to Stock and Uvnäs-Moberg (1988) (for further details see II and III). Plasma progesterone and E_2 concentrations were determined using an enzyme immunoassay and LH concentrations were measured using a heterologous RIA validated for porcine plasma (Forsberg et al, 1993) (for further details see IV and V).

4.6 Oestrus detection and ultrasonographic examination (IV, V)

From the day after weaning, oestrus detection was performed twice daily and the sows were considered to have reached the pro-oestrus phase when the first signs of vulva swelling and reddening were noted. Detection of the onset of oestrus was since performed every 4th hour using the back-pressure test in the presence of a boar. The onset of oestrus was estimated as midway between the last refusal and first acceptance to stand. During both oestrus cycles, the sows

were subjected to transrectal ultrasonographic examination to determine the time of ovulation. Ultrasonography was performed once daily from the onset of pro-oestrus until 20 h after the onset of standing oestrus, and thereafter every 4th hour until ovulation had occurred. The time of ovulation was defined as 2 h before the first time follicles were no longer visible or 2 h before the time when there was a marked reduction in the number of follicles.

4.7 Determination of ovulation rate (IV, V)

The genital tract of the sows was removed immediately after slaughter for examination. The number of *corpora lutea* was recorded in each ovary. By counting both the most recent and the older *corpora lutea*, the ovulation rate during the 1st and 2nd oestrus could be determined.

4.8 Variables

The daily litter weight gain as well as the average daily piglet weight gain within litter (litter weight gain divided by litter size) was calculated for 5 different periods during lactation: early postpartum period: (days 1 to 4 postpartum), early stabilised lactation (days 5 to 8 postpartum), peak lactation (around the time for nest-leaving; days 9 to 15 postpartum), peak lactation (after the time for nest-leaving) (days 16 to 22 postpartum) and declining lactation (day 23 postpartum to weaning). The various periods were used in the papers for comparisons with the respective variables of interest.

The following behavioural variables were determined by continuous observation from the videotapes, each representing a 24-h period: frequency of successful nursings; frequency of unsuccessful nursings; total nursing duration (sum of duration of all nursings); average duration of sow-terminated nursings; percentage of successful nursings that were terminated by the sow; average nasal contacts per piglet in a litter either not connected with nursings or in total. In addition, 5-min instantaneous sampling was used to determine percentage of observations when the sow was lying sternally (I-III, V).

Metabolic rate of the sows on days 7 and 21 was described using the following variables: pre- and postfeeding NEFA, urea, glucose and insulin, and mean prolactin and somatostatin concentrations. Prefeeding concentrations were estimated using the sample taken 30 min prior to the morning meal and postfeeding concentration using a mean of 7 samples from 15 to 210 min after

the morning meal. Sow weight loss was calculated for the periods between days 1 and 15 and between days 15 and 22 of lactation (I, II). The metabolic state during late lactation and after weaning was estimated using an average of the 2 daily samples (one sample daily after weaning) obtained from day 14 postpartum onwards (IV).

Hormonal variables from day 14 are expressed as means of values from 1 to 3 nursings per sow. For each of the 3 hormones (oxytocin, prolactin and somatostatin) 2 variables were calculated: mean non-nursing (NN) and mean nursing (N) concentrations (III).

For LH and E_2 on days 14 and 21 of lactation and on day 1 after weaning, the following variables were used: frequency of LH peaks and pulses (defined according to Tsuma et al. (1995)); LH base concentration (mean + 1 S.D. of all values excluding the peak values); LH average concentration (mean of all values) and average E_2 concentration (IV, V).

The average progesterone concentration was defined from the 2 daily samples separately for each of the last 3 weeks of lactation and for the 2 weeks after weaning (IV, V).

Variables estimating the postweaning reproductive success included: interval from weaning to 1st oestrus (h); interval from onset of oestrus to 1st ovulation (h); interval from 1st to 2nd oestrus (h); interval from onset of 2nd oestrus to ovulation (h); and number of corpora lutea at 1st and 2nd postweaning oestrus respectively (IV, V).

4.9 Statistical analyses

In papers I, IV and V statistical analyses were done with SAS (I, IV, V) (SAS v. 6.12, SAS Institute, 1997). Mixed models were used to examine changes in average daily weight gain and nursing behaviour throughout lactation, as well as effects of behaviour variables on piglet performance (I). To measure within-sow behavioural consistency between days of lactation, covariates between repeated measures were modelled as a 1st order autoregression process (AR (1)) (Ranta et al., 1994; SAS Institute, 1997). Correlations between different behavioural variables were tested separately for each day by simple Pearson's correlation coefficients.

The GLM procedure was used for data concerning postweaning reproductive performance and sow weight (IV, V). The GLM procedure for repeated measurements (SAS Institute, 1997) was used to analyse NEFA, progesterone

LH and E₂. As NEFA is closely linked to the metabolic level of an animal, and a better estimator of this than weight loss is, the analyses of associations between reproductive traits and catabolic level were based on NEFA concentration. Sows were divided into 2 equally sized groups retrospectively based on mean NEFA concentration during late lactation (starting day 14 post partum) and after weaning (until the 2nd oestrus) (IV) and b) mean nursing frequency, nursing duration and percentage of sow-terminated nursings of all nursings in middle and late lactation (days 13, 20 and 30 postpartum) (V). All statistical models included the effect of group.

In papers II and III, all statistical analyses were performed using SPSS for Windows, version 8.0 (SPSS inc., 1998). In paper II changes in physiological measures between weeks 1 and 3 were tested using Wilcoxon signed ranks tests and associations between the different physiological variables and between behavioural and physiological variables were examined using Spearman rank correlation coefficients. To test the effects of physiological state of the sow on piglet and litter growth, regression models were used (Ranta et al., 1997; SPSS Inc., 1998). The models included litter size and average piglet weight on day 1 postpartum as covariates.

To investigate the relationship between piglet mortality, catabolic state and sow behaviour, the sows were retrospectively divided into 2 groups according to the number of live-born piglets that died before weaning (II). Thus two groups were formed: a low-mortality group with one or no piglets dead and a high-mortality group with more than one piglet dead. Differences in litter characteristics, physiology and behaviour between these groups were tested using Mann-Whitney U-tests (Ranta et al., 1997; SPSS Inc., 1998).

The NN and N concentrations within each hormone were compared using pairwise Wilcoxon matched-sample nonparametric tests (III). The nonparametric Spearman rank correlation was used to find associations between hormones, behaviour, piglet growth, sow weight loss and NEFA concentration (Ranta et al., 1997; SPSS Inc., 1998).

4.10 Missing data

One of the 24 sows was excluded from the study due to severe leg problems. Another sow weaned her piglets at day 12 postpartum and was also excluded from the study. During preliminary analyses it was found that one of the litters showed extremely poor growth (average daily piglet weight more than 2 S.D.

beyond the mean) between days 15 and 22 postpartum, even though no external reasons could be found. Since including this sow in the analyses affected the results to a large extent, it was decided that she should be excluded on the basis of being an extreme outlier. Due to technical problems with the catheters and the video recorder, blood-sampling and behavioural observations were not performed on all days with all sows. Therefore, the sample sizes vary between different statistical analyses.



5. Results

5.1 Litter statistics

The 21 experimental sows produced a total of 258 piglets, including stillborn (mean = 12.3, S.D. = 3.5, range = 6-19 piglets). The total number of piglets born alive was 228 (mean = 10.9, S.D. = 2.7, range = 6-14 piglets) and average piglet weight on day 1 postpartum was 1.48 kg (S.D. = 0.30 kg). The preweaning mortality (of live-born piglets) was 15% (n = 33); of these piglets, 31 died before day 4 postpartum and 2 after day 8 postpartum. The causes for death were, according to post mortem investigations, crushing (n = 16), starvation (n = 3), a combination of these (n = 7) and other causes (n = 4). For the remaining 3 piglets, the cause of death could not be determined in the post-mortem examination.

5.2 Pattern of nursing behaviour

Nursing behaviour during the various periods of lactation is described in Figure 5a-f. There was a strong significant effect of day on all behavioural variables ($p < 0.001$ for all). The autoregression coefficients indicated a rather high within-sow repeatability of the different variables, being highest for percentage of nursings terminated by the sow (AR (1) = 0.73) and lowest for the average duration of sow-terminated nursings (AR (1) = 0.35) (for further details see I).

5.3 Changes in metabolite and hormone concentrations and sow weight loss

Data concerning weight loss and hormonal and metabolic measures indicated a higher catabolic level during week 3 than during week 1 of lactation (Table

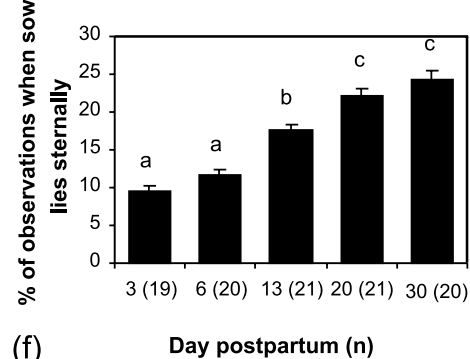
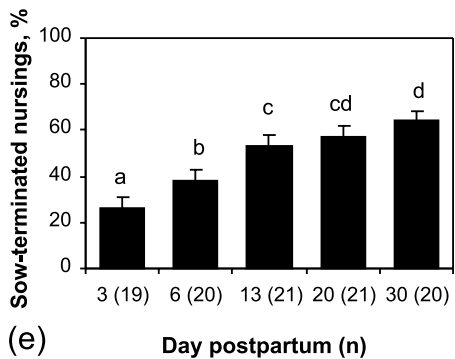
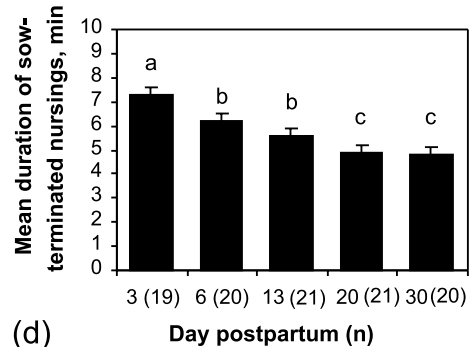
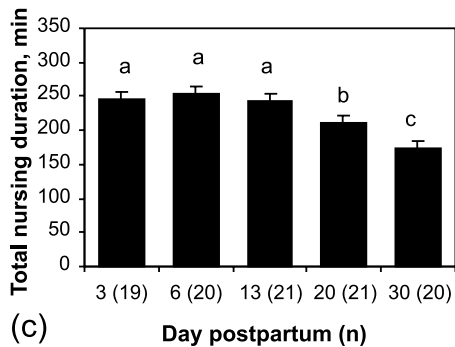
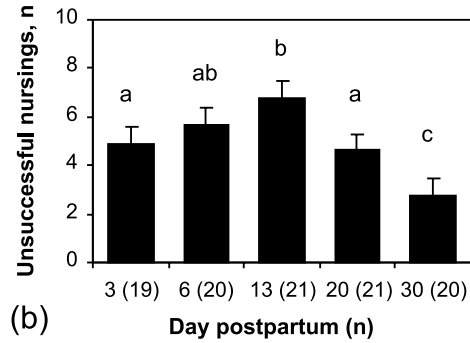
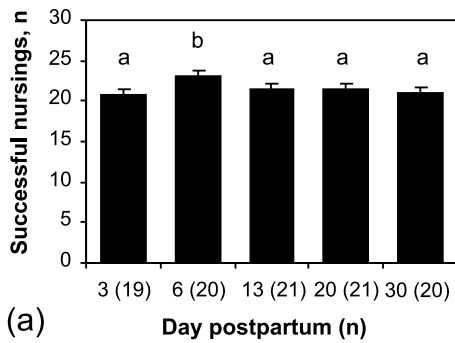


Figure 5 a-f. Changes in nursing behaviour (LSM and S.E.M.) on the 5 different observational days. a) Frequency of successful nursings, b) Frequency of unsuccessful nursings, c) Total duration of all nursings (min), d) Average duration of sow-terminated nursings (min), e) % of sow-terminated nursings of all nursings, f) % of observations when sow is in sternal recumbency. Bars lacking common letters differ ($p < 0.05$).

1). Figure 6a-d shows the pattern of changes in metabolite and hormonal concentrations during the 2 sampling days in one representative sow (sow 977).

Table 1. Medians (and interquartile ranges) of sow weight loss and metabolite and hormone concentrations during week 1 and week 3 of lactation (n = 18).

	Week1	Week 3	p-value
Sow weight loss ^a (g/day)	214 (750)	1107 (928)	0.001
Prefeeding NEFA ^b (mmol/l)	0.11 (0.07)	0.28 (0.26)	0.001
Postfeeding NEFA ^c (mmol/l)	0.07 (0.03)	0.11 (0.11)	0.001
Prefeeding urea ^b (mmol/l)	4.41 (1.44)	4.57 (1.24)	0.18
Postfeeding urea ^c (mmol/l)	4.55 (1.44)	4.77 (1.50)	0.03
Prefeeding glucose ^b (mmol/l)	5.12 (0.75)	4.23 (1.07)	0.001
Postfeeding glucose ^c (mmol/l)	5.75 (0.66)	5.67 (0.94)	0.78
Prefeeding insulin ^b (μU/l)	8.35 (7.17)	6.37 (4.48)	0.004
Postfeeding insulin ^c (μU/l)	58.3 (30.3)	60.0 (30.0)	0.59
Mean somatostatin ^d (pmol/l)	11.9 (6.69)	11.0 (7.94)	0.42
Mean prolactin ^d (ng/ml)	78.3 (42.4)	59.8 (32.6)	< 0.001

^a average daily weight loss for days 1-15 pp and days 15-22 pp

^b one morning sample

^c mean of 7 morning samples

^d mean of 25 samples spread over the day

5.4 Different measures of the metabolic state

Correlations between the different measures of the metabolic state have been reported in detail (in II). The clearest finding was that the NEFA concentration showed a strong positive correlation with sow weight loss during the 1st week of lactation ($r_s = 0.61$, $p = 0.007$ for prefeeding NEFA and $r_s = 0.75$, $p < 0.001$ for postfeeding NEFA). The correlation between sow weight loss and urea was opposite and not as strong ($r_s = -0.49$, $p = 0.04$ for prefeeding urea and $r_s = -0.52$, $p = 0.03$ for postfeeding urea).

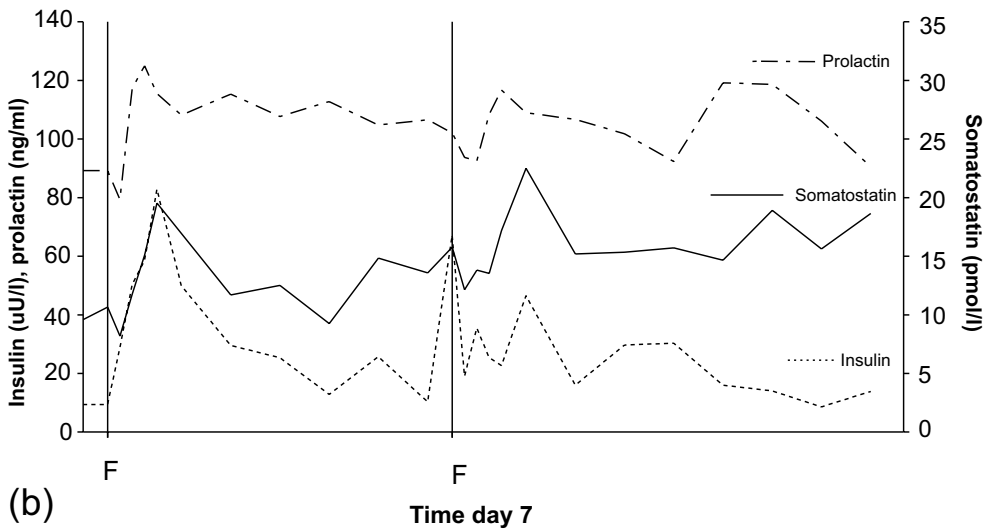
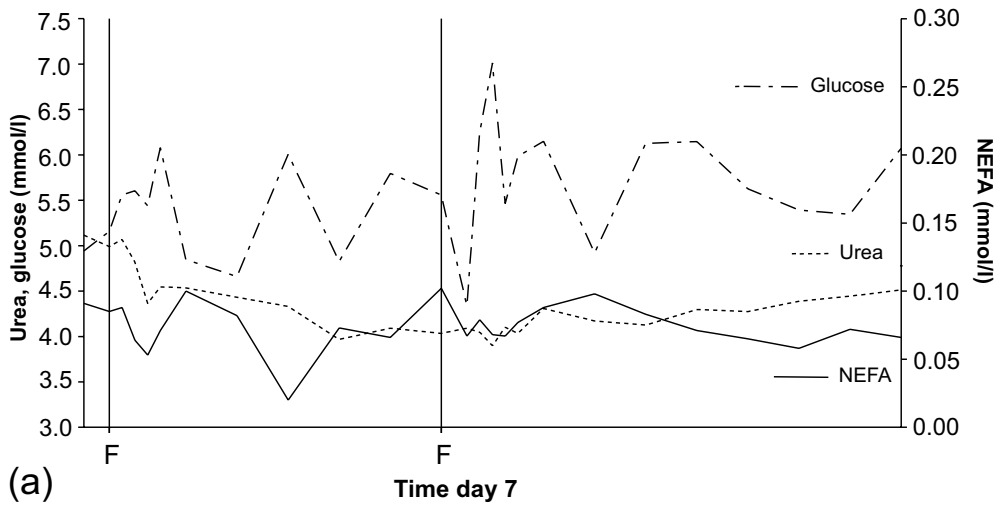


Figure 6 a-b. Patterns of metabolites and hormones in a representative sow (sow 977) during a 16-h period on day 7 postpartum. F indicates feeding time.

5.5 Metabolic state of the sow and nursing behaviour

During week 1 of lactation, the prefeeding insulin concentration tended to correlate positively with the percentage of observations the sow spent in sternal recumbency ($r_s = 0.45$, $p = 0.05$). There was also a slight tendency for prefeeding insulin to correlate with percentage of nursings terminated by the sow ($r_s = 0.39$, $p = 0.11$). When excluding one extreme sow that terminated

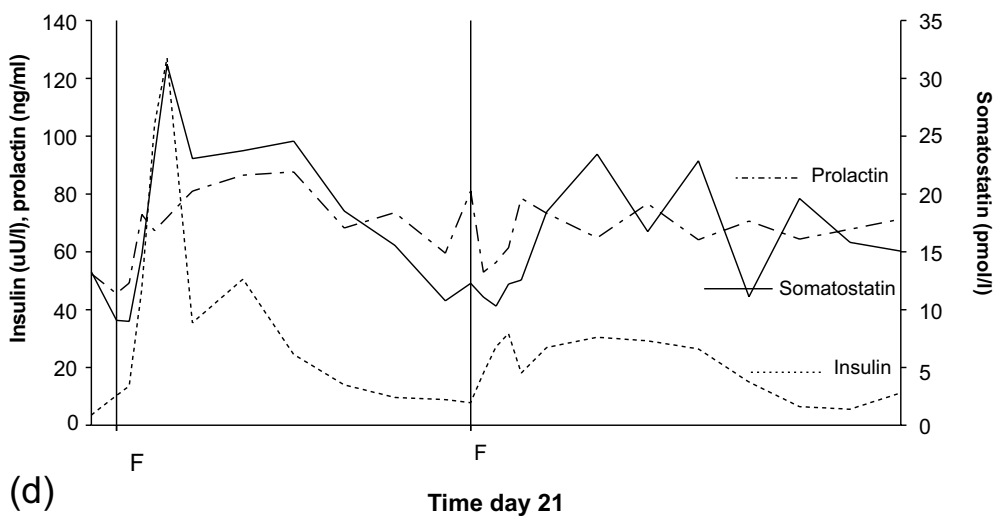
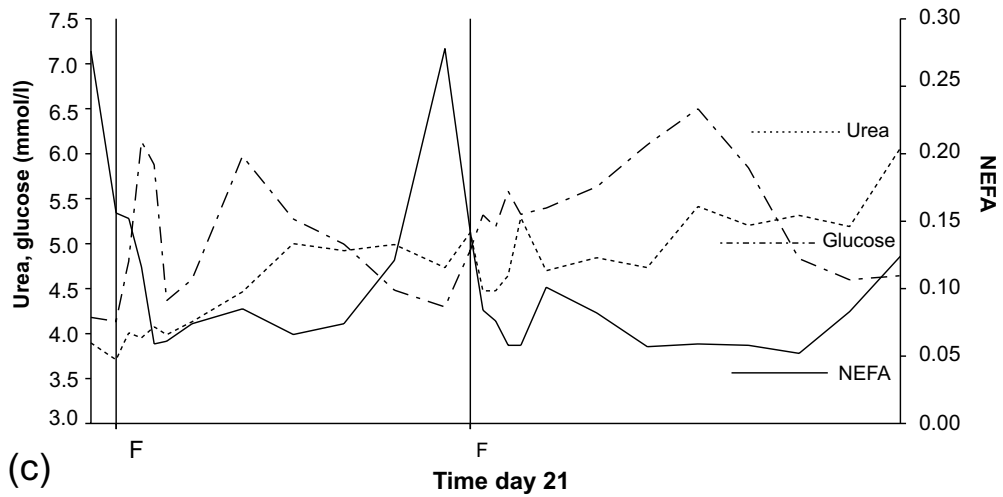


Figure 6 c-d. Patterns of metabolites and hormones in a representative sow (sow 977) during a 16-h period on day 21 postpartum. F indicates feeding time.

100% of nursings on day 6, this correlation was significantly positive ($r_s = 0.65$, $p = 0.005$). No other correlations between physiological measures and behaviour were found during the 1st week of lactation ($p > 0.1$ for all), except for a tendency for prolactin to correlate positively with total nursing duration ($r_s = 0.39$, $p = 0.09$).

Later in lactation (week 3), the postfeeding insulin concentration correlated negatively with successful nursing frequency ($r_s = -0.50$, $p = 0.04$), percentage of nursings terminated by the sow ($r_s = -0.65$, $p = 0.004$) and with

percentage of observations the sow spent in sternal recumbency ($r_s = -0.52$, $p = 0.03$) and tended to correlate negatively with the average duration of sow-terminated nursings ($r_s = -0.45$, $p = 0.06$). The prolactin concentration correlated positively with the frequency of unsuccessful nursings ($r_s = 0.60$, $p = 0.009$). No other correlations between the physiological measures and behaviour were found during week 3 of lactation ($p > 0.1$ for all).

5.6 Effect of nursing behaviour on average piglet weight gain

Successful nursing frequency had a significantly positive effect on average piglet weight gain; one additional successful nursing over 24 h was estimated to increase average daily piglet weight gain by 5.12 g ($p = 0.02$). None of the other behavioural variables significantly affected average daily piglet weight gain ($p > 0.1$ for all).

5.7 Effect of metabolic state of the sow on piglet and litter weight gain

None of the measured metabolites, hormones or sow weight loss affected average piglet or litter weight gain during the 1st week of lactation ($p > 0.1$ for all). During week 3 litter weight gain was positively affected by the postfeeding NEFA concentration ($p = 0.03$) while the prefeeding NEFA concentration also tended to affect litter weight gain positively ($p = 0.09$). In addition, the postfeeding insulin concentration affected average piglet weight gain positively ($p = 0.03$), and post-feeding glucose concentration litter weight gain positively ($p = 0.04$). Sow weight loss had a positive effect on average piglet weight gain during this week ($p = 0.02$), i.e. high sow weight loss correlated with high average piglet weight gain.

5.8 Differences in weight loss, metabolite and hormonal concentrations, and nursing behaviour between sows with low or high mortality

The sows were divided into a low-mortality group with none or one piglet dead per litter of live-born piglets ($n = 12$) and a high-mortality group with more than one piglet dead ($n = 9$). The litter size was larger and individual piglets weighed less on average at birth in high- than in low-mortality litters.

Table 2. Medians (and interquartile ranges) of litter characteristics after farrowing in the low-mortality and high-mortality groups. P-values refer to differences between groups (n = 21).

	Low- mortality	High- mortality	p-value
Total number born	10.5 (5)	15 (4)	0.004
Number born alive	9 (5)	13 (2)	0.004
Number born dead	0 (1)	1 (4)	0.28
Piglet mortality (n)	1 (1)	3 (2)	< 0.001
Mean live-born piglet birth weight (g)	1530 (411)	1350 (308)	0.02
Total live-born litter weight (kg)	14.3 (5.6)	16.2 (4.1)	0.22

Differences in litter characteristics at farrowing between the 2 mortality groups are presented in Table 2. Sows with low mortality in their litters had higher weight loss and NEFA concentration than sows in the high-mortality group during the 1st week of lactation. Piglets from high-mortality litters grew more slowly during week 3 than piglets in low-mortality litters. Differences in litter performance, sow weight loss and metabolic state between the 2 groups are presented in Tables 3a and b. None of the behavioural variables differed between mortality groups ($p \gg 0.1$).

5.9 Nursing-induced changes in lactation-related hormones on day 14

The mean (S.D.) NN oxytocin level was lower than the N oxytocin level ($p = 0.002$). In contrast, the NN prolactin level was higher than the N prolactin level ($p = 0.005$), while NN somatostatin did not differ from N somatostatin ($p = 0.65$). The somatostatin values were, therefore, pooled into an overall somatostatin concentration. Hormone concentrations during the observation period for 3 representative sows are shown in Figure 7a-c.

Table 3a. Medians (and interquartile ranges) of litter performance, sow weight loss, metabolites and hormones in week 1 of lactation in the low-mortality and high-mortality groups. Number of observations varies between 18 and 21.

	Week 1		p-value ^a
	Low-mortality	High-mortality	
Litter size	8 (4)	10 (2)	0.31
Piglet weight gain(g/day)	233 (67)	213 (71)	0.25
Litter weight (g/day)gain	2214 (1019)	2153(499)	0.81
Sow weight loss ^b (g/day)	589 (267)	-143 (375)	< 0.001
Prefeeding NEFA ^d (mmol/l)	0.13 (0.09)	0.07 (0.04)	0.002
Postfeeding NEFA ^e (mmol/l)	0.08 (0.03)	0.06 (0.01)	0.006
Prefeeding urea ^d (mmol/l)	4.19 (1.33)	4.99 (1.50)	0.05
Postfeeding urea ^e (mmol/l)	4.03 (1.25)	4.72 (1.23)	0.05
Prefeeding glucose ^d (mmol/l)	5.51 (0.95)	5.01 (0.43)	0.20
Postfeeding glucose ^e (mmol/l)	6.08 (0.59)	5.49 (0.88)	0.63
Prefeeding insulin ^d (μU/l)	11.3 (8.22)	7.83 (2.44)	0.33
Postfeeding insulin ^e (μU/l)	63.3 (31.1)	46.5 (27.2)	0.10
Mean somatostatin ^c (pmol/l)	11.6 (6.74)	13.8 (9.22)	0.60
Mean prolactin ^c (ng/ml)	78.9 (49.8)	91.53 (39.4)	0.94

^a p-values refer to differences between groups

^b average daily weight loss for day 1-15 pp and day 15-22 pp (negative value indicates weight gain)

^c mean of 25 samples spread over the day

^d one morning sample

^e mean of 6 morning and 6 afternoon samples

Table 3b. Medians (and interquartile ranges) of litter performance, sow weight loss, metabolites and hormones in week 3 of lactation in the low-mortality and high-mortality groups. Number of observations varies between 18 and 21.

	Week 3		p-value ^a
	Low-mortality	High-mortality	
Litter size	8(4)	10 (2)	0.31
Piglet weight gain(g/day)	337 (89)	270 (44)	< 0.001
Litter weight (g/day)gain	2764 (836)	2714 (622)	0.25
Sow weight loss ^b (g/day)	1107(1286)	1071 (1125)	0.27
Prefeeding NEFA ^d (mmol/l)	0.40 (0.27)	0.19 (0.15)	0.06
Postfeeding NEFA ^e (mmol/l)	0.14 (0.11)	0.08 (0.06)	0.03
Prefeeding urea ^d (mmol/l)	4.51 (1.16)	4.94 (2.31)	0.41
Postfeeding urea ^e (mmol/l)	4.49 (1.69)	5.07 (2.1)	0.27
Prefeeding glucose ^d (mmol/l)	4.23 (1.40)	4.32 (1.49)	0.63
Postfeeding glucose ^e (mmol/l)	5.63 (1.18)	5.69 (1.52)	0.97
Prefeeding insulin ^d (μU/l)	5.61 (4.54)	6.37 (8.25)	0.76
Postfeeding insulin ^e (μU/l)	55.9 (26.0)	60.2 (33.9)	0.90
Mean somatostatin ^c (pmol/l)	10.8 (7.84)	13.0 (9.80)	0.52
Mean prolactin ^c (ng/ml)	56.6 (30.7)	63.9 (33.2)	0.63

^a p-values refer to differences between groups

^b average daily weight loss for day 1-15 pp and day 15-22 pp (negative value indicates weight gain)

^c mean of 25 samples spread over the day

^d one morning sample

^e mean of 6 morning and 6 afternoon samples

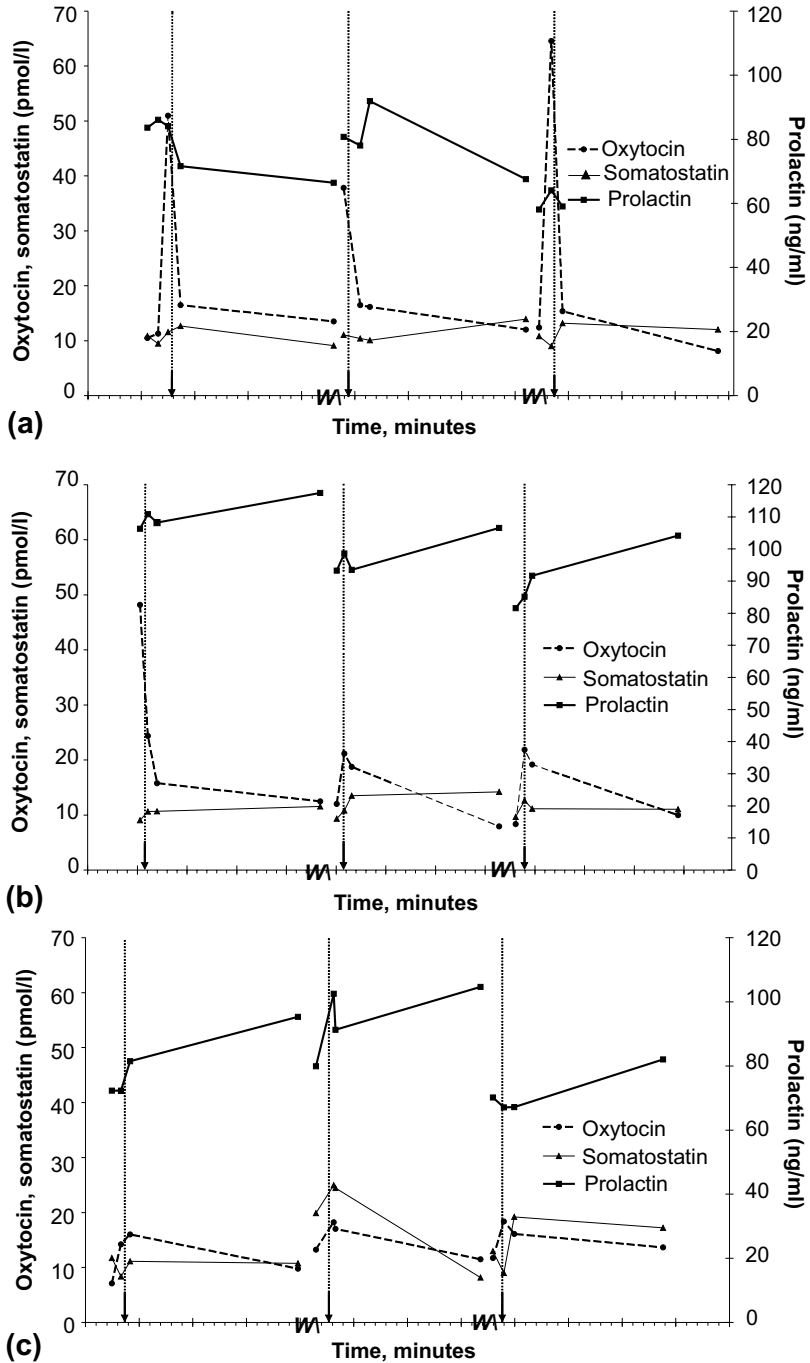


Figure 7 a-c. Concentrations of oxytocin, somatostatin and prolactin in 3 sample sows during 3 successful nursings. Vertical lines with arrows represent milk ejections. The 1st sample during each nursing was drawn when the premessage began and the last 15 min after the end of the nursing.

Table 4. Spearman rank correlation coefficients (r_s) and p-values for the correlation between lactation-related hormone concentrations and sow and litter performance. Number of observations varies between 15 and 19.

		Litter size day 15	Daily piglet weight gain	Daily litter weight gain	Sow weight loss	NEFA concentration	Nursing frequency
Nonnursing prolactin (ng/ml)	r_s	-0.14	0.01	-0.08	0.33	0.29	0.07
	p	0.57	0.96	0.75	0.20	0.22	0.76
Nursing prolactin (ng/ml)	r_s	-0.12	-0.02	-0.11	0.25	0.28	0.07
	p	0.62	0.94	0.66	0.34	0.25	0.77
Somatostatin (pmol/l)	r_s	0.28	-0.15	0.05	-0.46	-0.12	0.25
	p	0.28	0.57	0.86	0.08	0.65	0.34
Nonnursing oxytocin (pmol/l)	r_s	0.26	0.50	0.45	0.06	0.20	-0.18
	p	0.29	0.03	0.05	0.80	0.41	0.46
Nursing oxytocin (pmol/l)	r_s	0.16	0.19	0.31	0.52	0.56	-0.35
	p	0.51	0.45	0.20	0.03	0.01	0.14

5.10 Hormonal concentrations and the sows' use of resources for milk output

The NN oxytocin level was positively correlated with average piglet and with litter weight gain. In addition, the N oxytocin level was positively correlated with sow weight loss and NEFA concentration. Neither prolactin nor somatostatin correlated with any of the measures for sow resource use and milk output. The correlation coefficients and significance levels between concentrations of lactation-related hormones and sow and litter performances are presented in Table 4.

5.11 Oxytocin and prolactin concentrations and the sows' piglet-directed behaviour

The only significant correlation between oxytocin and prolactin on one hand and the measures of piglet-directed behaviour on the other was a positive cor-

Table 5. Spearman rank correlation coefficients (r_s) and p-values for the correlation between oxytocin concentrations and measures of piglet-directed behaviour. Number of observations varies between 17 and 19.

		Total number of nasal contacts / piglet	Number of nasal contacts excl. nursings / piglet	% sow- terminated nursings	Duration of sow- terminated nursings	% sternal recumbency
Nonnursing oxytocin (pmol/l)	r_s	-0.39	-0.14	0.50	-0.10	0.22
	p	0.13	0.60	0.03	0.69	0.36
Nursing oxytocin (pmol/l)	r_s	0.08	0.21	-0.20	-0.30	0.07
	p	0.77	0.42	0.40	0.21	0.78
Nonnursing prolactin (ng/ml)	r_s	0.22	0.14	-0.27	-0.36	-0.09
	p	0.39	0.60	0.26	0.13	0.72
Nursing prolactin (ng/ml)	r_s	0.32	-0.11	-0.18	-0.27	-0.13
	p	0.21	0.66	0.47	0.26	0.59

relation between NN oxytocin levels and percentage of observations the sow spent lying sternally. The correlation coefficients and significance levels between measures of piglet-directed behaviour and oxytocin as well as prolactin concentrations are presented in Table 5.

5.12 Differences in reproductive functions between sows with high and low catabolic rates during lactation

Sows in the high NEFA-concentration group lost more weight during lactation than sows in the group with low NEFA concentrations (on average 31 kg and 8 kg respectively from farrowing to weaning, $p < 0.001$), although there was no significant difference in sow body weight between these groups at any point ($p \gg 0.1$)

Progesterone, LH and E_2 concentrations did not differ significantly between the two catabolism groups ($p > 0.05$), neither during lactation nor after weaning. No differences in the fertility measures were found between groups, except for a tendency towards increased duration between the onset of oestrus

and 1st ovulation in the high-NEFA compared with the low-NEFA group ($p = 0.08$) (for further more details see IV).

5.13 Differences in reproductive functions between sows with differing nursing behaviour

The average LH concentration was higher on both days 14 and 21 of lactation in the short than in the long nursing-duration group ($p = 0.03$ and 0.01 respectively). The same was found for basal LH concentration ($p = 0.08$ and 0.03 , respectively, on days 14 and 21). The E_2 concentration was higher in the short than in the long nursing-duration group on the day after weaning ($p = 0.03$). No other hormonal or fertility measures differed significantly between the groups (for further details see V). The groups based on nursing frequency and proportion of sow-terminated nursings revealed no significant differences ($p > 0.1$) and these results are thus not reported.



6. Discussion

6.1 Methodological considerations

The sows used in the present study were commonly used Yorkshire sows and since their housing and management resembled normal practice as far as possible, the results are reasonably representative of a production setting. Sows were loose-housed during the entire study period, which is the practice in Sweden, but not in many other countries. Since maternal behaviour is altered by the environment (Thodberg, 2001), similar results may not be obtained in sows confined to crates or kept more extensively (e.g. outdoor sows). More research is needed to further investigate maternal abilities in different environments.

Sows synchronise their nursing behaviour when kept in groups (Watson and Bertram, 1980; Wechsler and Brodmann, 1996) and it is therefore probable that the sows in this study influenced each other. The sows were kept in order to minimise physical contact, but there was no sound isolation between the sows. Effect of batch on the different variables was tested in preliminary analyses (not reported here) and as no significant effects were found, it was decided not to include batch effect in most of the further analyses.

The sample size, statistical approach and descriptive nature of the present study impose severe restrictions on the interpretation of the results. Firstly, the type of study design used does not allow for conclusions to be drawn regarding causal relationships. Secondly, the study included a great number of statistical tests (which can increase the experiment-wise error) and several different statistical approaches were used to test the different hypothesis. The aim was to use methods that gave the most reliable result, considering characteristics of the data set, such as clear deviations from a normal distribution and the limited sample size. In addition, many of the reported significance levels are rather low. Keeping in mind these restrictions of the study

design and the statistical weaknesses, results must be interpreted with care and considering their biological relevance. However, the results presented here give good indications of the phenomena needing further investigation in more experimental studies.

Since this study focused on the sow and her characteristics, we were not able to standardise for litter effects. Differing litter sizes and litter characteristics, such as vitality, behavioural activity and competition between siblings, probably have a large effect on the sow, and the interaction between sow and piglets should be studied further. In some of the statistical models we have adjusted for litter characteristics, such as litter size and average piglet body weight (e.g. I, II), in other approaches we have looked at both litter and average piglet weight gain (see e.g. III). Neither approach is optimal, but, again, the selection of models had to be done considering restrictions of the data set. In addition, correlation between the dependent variable and litter size was always tested in preliminary analyses, not reported here (e.g. III). If the correlation was very weak or non-existent, as was the case for correlations between litter size and oxytocin, prolactin and somatostatin concentrations, we felt rather safe not including litter size in further models.

The division of sows retrospectively into categorical groups based on continuous variables might not be the most optimal method to analyse this kind of data. Similar analyses have, however been used in several previously published studies of descriptive nature (e.g. Rojkittikhun et al, 1992 (NEFA concentration); Sterning et al., 1997 (sow weight loss); De Passillé and Rushen, 1989 (piglet mortality). The distribution of mean NEFA concentration within the data set indicated bimodality of the variable (results not reported here) and thus allowed for a reasonably clear division into two separate groups. Sows that did not clearly fit into either group were assigned to the closest one, giving two equally-sized groups. In order to follow the same analytical pattern, the same method was used also in V, although the behavioural variables were not as clearly bimodal. The reason for dividing sows into two groups based on piglet mortality (III), on the other hand, was more purely biological; it was considered that one piglet dead per litter is biologically (and economically) acceptable, while anything more can be considered as unnecessarily high.

One aim of the present study was to determine those individual maternal characteristics that possibly could be used as selection criteria when aiming at breeding for good maternal abilities. We reported sow traits that appear to be

stable within one lactation (e.g. nursing behaviour) and probably are truly maternal characteristics (e.g. oxytocin concentration), but these may be affected to a great extent by factors occurring during the lactation in question. Factors that can influence maternal characteristics include litter size and piglet vitality, sow health, feeding regime, environmental conditions and management practices. Therefore, it would be of great importance to study these characteristics in sows during several lactations. The next step would then be to study the heritability of maternal characteristics.

The first few days of lactation are crucial for the development and survival of piglets (De Passillé and Rushen, 1989), and the level of colostrum intake during parturition and the early hours of life is of great importance for the piglets' success. Piglets are born with very small energy reserves and a poor immunodefence and a low early growth of piglets has been found to be associated with low levels of immunoglobulins (De Passillé et al., 1988). Milk production during the early days is also of great importance and to a large extent determines the growth rate later on (Thompson and Fraser, 1988). Hormonal changes during parturition are rapid and major and will probably also exert effects during lactation. One weakness of our study is therefore that we obtained very little information during the first days postpartum. This compromise was chosen so as not to disturb sows during this important period, but for a better understanding of sow maternal characteristics, data should also be collected during and directly after the parturition period.

One important aspect of sow maternal behaviour was not included in this thesis: As a large percentage of piglet mortality is caused by crushing (Glastonbury, 1977; Edwards et al., 1986; Dyck and Swierstra, 1987; Edwards et al., 1994) behaviour related to crushing could have been included as one measure of maternal behaviour. However, the main focus of this thesis was to describe maternal characteristics related to milk production and piglet growth. The focus on piglet mortality in this study is thus mainly put on mortality due to starvation. Linked to this study, results on behaviour before and during lying-down will be reported separately (Valros, et al, *unpublished*).

6.2 Patterns of nursing behaviour

The reported changes in nursing behaviour during lactation indicate an early initiation of the weaning process (I). Even though we did not find a decrease in successful nursing frequency with proceeding lactation, which has been re-

ported as a sign of an ongoing weaning process in sows under less restricted conditions (Jensen, 1988; Bøe, 1991), we found other indicators of decreasing maternal investment. Firstly, the total time spent nursing decreased from day 13 postpartum onwards, mainly due to an increase in the percentage and a decrease in the duration of sow-terminated nursings. This shows that the sows allow less massage at later stages of lactation. The steady increase in percentage of sow-terminated nursings over the entire lactation confirms a pattern found in earlier studies (Watson and Bertram, 1980; Jensen, 1988). Secondly, the percentage of observations when the sow was lying sternally, on the udder, increased with proceeding lactation, a pattern that has also been reported by Götz (1991). By lying on the udder the sow can reduce the possibility for massaging by the piglets.

The housing conditions affect maternal behaviour in sows (Castrén et al., 1989; Thodberg et al., 2002) and it is possible that lowering of the nursing frequency as a method of weaning may be used more clearly by sows able to walk away from their piglets (e.g. Jensen, 1988; Bøe, 1991). As in our findings, Götz (1991) did not find nursing frequency to decrease towards the end of a 4-week lactation, when studying sows in farrowing crates. Sternal recumbency and shorter allowance of udder massage may be used by crated or penned sows that cannot move away from the nursing stimulus provided by their litters.

Our results indicate that sows do have different, individually stable behaviour patterns, at least within one lactation. If this is also true for subsequent lactations and maternal behaviour really is an individual characteristic, it gives further value to any effect of sow behaviour on piglet growth. Therefore, this finding encourages further studies into the heritability of maternal behaviour in sows. On the other hand, Špinková et al. (2002) found only low repeatabilities both within and between lactation periods for variables characterising nursing frequency and the willingness of the sow to allow udder massage. The same authors found that the patterns of nursing vocalisations were highly repeatable. The contrasting results imply a need for further studies of the individual stability of sow nursing behaviour.

6.3 Physiological changes in the sow during lactation

Sows appear to be in a state of higher catabolism during peak lactation (week 3) than during the 1st week of lactation (II). Several measures of the metabolic

state support the finding of this study: sows had higher concentrations of NEFA and urea and lower levels of glucose and insulin during the 3rd week than during the 1st. The negative energy balance resulted in increasing sow weight loss from week 1 to week 3, which is in accordance with earlier results (Rojkittikhun et al., 1993a; Kraetzl et al., 1998), although the observations have not been consistent so far; the opposite pattern has also been observed (Hultén et al., 1993).

As milk production increases from week 1 to week 3 (seen as higher piglet weight gain; II), the demand for nutrients by the mammary gland increases. It is therefore possible that the declining concentration of glucose indicates an increased proportion of the glucose intake being used by the mammary gland for milk production, and the decreasing prefeeding insulin concentration may be merely a physiological result of this lower blood glucose concentration (Rojkittikhun et al., 1993a). Alternatively, the lowered prefeeding insulin concentration occurring later in lactation can be a reflection of increased insulin utilisation by the mammary gland at this time of high milk production.

Even though milk production, measured as piglet weight gain, was higher during week 3 than week 1 of lactation, the prolactin concentrations were lower at this point. This could be due to the fact that the total nursing duration was lower during week 3 than week 1 (I), since the prolactin concentration is positively correlated with nursing duration (II; Algers et al., 1991; Špinka et al., 1999).

The urea concentrations, although slightly higher during week 3 than during week 1, were still not high enough on either day to imply any major protein store mobilisation (Kraetzl et al., 1998). Since NEFA was the metabolite most strongly correlated with sow weight loss (II), at least during week 1 of lactation, it appears that most of the early weight loss was due to usage of body fat reserves for milk production. Our results support the notion that NEFA is an appropriate measure of the sow's metabolic state.

6.4 Sow metabolism and piglet growth and survival

The higher NEFA concentrations and weight loss in sows with low mortality in their litters could be a sign of a high capacity by the sow to effectively switch to a catabolic state, thus having higher milk production and less risk of piglet starvation early in lactation. This is further supported by the fact that both NEFA concentration and average daily piglet weight gain later in lacta-

tion were higher in those sows with low mortality in their litters. Early weight gain is important for both survival and later performance (De Passillé and Rushen, 1989).

We measured NEFA concentrations as late as on day 7, while most of the mortality occurs during the first 4 days of lactation. Hence, these results are only speculative, but do suggest the importance of the sow switching from an anabolic to a catabolic state as soon as possible following parturition. This switch may be influenced by the early oxytocin level, since oxytocin was found to correlate positively with NEFA concentration (III). Incidences during and directly after parturition, e.g. stress during parturition (Lawrence et al., 1995), prolonged parturition (Castrén et al., 1993b) and probably also piglet vitality at birth can influence oxytocin levels; therefore, these early days during and immediately following parturition should be examined more carefully.

No association between litter or average piglet weight gain and catabolic state was found during week 1 of lactation; neither did litter size appear to limit piglet growth at this time (II). Later in lactation, when milk production has attained its peak and the demand on the sow was higher, there was an association between high milk output (measured as litter weight gain) and high level of NEFA. At this time, litter size also became restrictive, with piglets in smaller litters growing faster than those in large litters.

6.5 Associations between sow behaviour and metabolism

In the present study, we found evidence for a connection between insulin concentrations and sow behaviour, especially during the 1st week of lactation (II), a stage when milk production was still increasing (Toner et al., 1996). It appeared that a high level of insulin was associated with the sow performing much massage-avoiding behaviour, i.e. lying frequently on the udder and terminating a large percentage of nursings. This association between insulin and massage avoidance could have been mediated through the prolactin concentration. One possible explanation is that allowance of much udder massage increases prolactin secretion (Špinka et al., 1999), and thus efficiency of the udder in utilising insulin (Rojkittikhun et al., 1992). This is supported by the tendency, in the present study, for prolactin to correlate positively with total nursing duration (II), and by earlier reports showing a positive correlation between nursing duration and prolactin concentration (Algers et al., 1991).

Therefore, a high motivation to avoid udder massage may cause (or be

caused by) low prolactin concentrations, and thus a reduced number of insulin receptors in the udder and higher concentrations of insulin in the blood. This is further supported by the fact that a manipulated high frequency of nursings has been shown to decrease the baseline insulin concentration (Špinka et al., 1999). On the other hand, the association between insulin and nursing behaviour was very different during the 3rd week of lactation compared with during week 1, making the results difficult to interpret.

6.6 Associations between nursing behaviour and piglet weight gain

Several studies have shown that increased nursing frequency improves milk production in pigs (Špinka, 1997; Sinclair, 1998; Auldism et al., 2000). These studies have used either manipulated nursing intervals (Špinka et al., 1997) or cross-suckling of litters (Auldism et al., 2000). In addition, Sinclair et al. (1998) showed that high-milking Meishan sows have higher nursing frequency than European White sows. The fact that we found similar (although statistically not very strong) evidence in a comparison between sows of the same breed, and without any experimental manipulations of sow behaviour or litter characteristics, confirms these more experimental findings (I). In addition, we found nursing frequency to be repeatable within sows during one lactation and the effect on piglet growth to be similar throughout lactation. Hence, we hypothesise that altering the nursing frequency could be an individual strategy used by sows to influence milk production. Even though one additional nursing was associated with an increase in piglet growth comparable to a decrease of one piglet in the litter (increase in average daily piglet weight gain per added nursing was 5.1 g and 4.3 g per decrease in litter size by one piglet), the between-sow variation in nursing frequency was rather low. It is therefore unclear whether the results really have any practical implications. It is possible that the importance of these findings is more relevant when sows are housed more unrestrainedly, since the variation in behaviour between sows is thus greater (e.g. in loose-housing systems (Bøe, 1994).

The data on individual milk intake collected by Špinka et al. (1997) suggested that the alveoli can fill up with milk quickly after each successful nursing. Hence the authors hypothesised milk yield to be mainly determined by the frequency of emptying of the alveoli and by the completeness of the emptying. In addition, Auldism et al. (2000) found a positive correlation between

milk yield and gland weight and a higher individual gland weight in more frequently nursed sows. This indicates that milk production is strongly influenced by behavioural aspects affecting the frequency of milk letdown. Taking into account the lack of correlation between nursing frequency and total nursing duration in our study and the fact that we did not find an effect of total nursing duration on piglet growth (I), it is likely that the positive effect of nursing frequency on piglet growth was mainly caused by the high frequency of milk ejections per se, not by a longer total duration of udder massage. Therefore, we suggest that by changing nursing frequency, the sow can influence the milk output and thus investment in her present offspring.

6.7 Oxytocin, prolactin, somatostatin and milk production

The hormone oxytocin is known to play an important role in milk production. It has been shown in several studies that oxytocin triggers milk production (for a review see Goodman and Grosvenor, 1983). Oxytocin increases just before milk letdown during the majority of successful nursings (Ellendorff et al., 1982; Rojittikhun et al., 1993b). This nursing-related burst in oxytocin release is brief and only occurs if sufficient stimulation is provided by piglets massaging the udder (Algers et al., 1990). Also in paper III of the present study an increased concentration of oxytocin was seen during nursings, although the blood sampling schedule did not allow for exact estimations of peak values.

In the present study we were able to show indications of a more complex role played by oxytocin during lactation (III). High concentrations of oxytocin outside nursings correlated with high average piglet weight gain. This relationship between oxytocin and milk production may be mediated via the metabolic effects of oxytocin, since we also found that oxytocin concentrations during nursings were positively associated with high sow weight loss and high concentrations of NEFA. In rats, Björkstrand et al. (1996) indicated that elevated concentrations of circulating oxytocin increased the use of body reserves (i.e. increased levels of glucose and glucagon) and thus likely increased the mobilisation of glucose for milk production. In addition, oxytocin appears to be associated with NEFA concentrations in rats (Suva et al., 1980). Considering this evidence and the results in III, it appears likely that oxytocin concentrations, both during and outside nursings, increase the use of body reserves for milk production. As was shown in II, a high level of catabolism dur-

ing early lactation is associated with high piglet weight gain. We therefore hypothesise that high levels of oxytocin relate to good piglet growth via positive effects on the maternal metabolism. In addition, oxytocin may influence milk production directly at the level of the mammary gland by affecting the productivity or maintenance of mammary epithelial cells positively (Ballou et al., 1993). Since there has been no evidence so far that piglets can influence the oxytocin concentration (e.g. Algers et al., 1990), we also hypothesise that this is mainly a maternal characteristic. It must be emphasised that our results only show associational relationships, and therefore further experimental studies are needed to enable us to draw any conclusions on causal relationships.

Even though prolactin increased in response to nursings (III) and correlated with nursing duration (II), as has been reported previously (Algers et al., 1991; Rushen et al., 1993; Špinka et al., 1999), we failed to find evidence for a quantitative relationship between prolactin concentration and resource use for milk production (III). It is possible that even though prolactin plays an important role in the initiation and maintenance of lactation (Barber et al., 1992; Flint et al., 1995; Farmer et al., 1998), the function is of ‘all-or-nothing’ nature. In other words, there may be a threshold concentration of prolactin needed for normal milk production, but any increases from this level cannot further enhance milk production. Prolactin declines rapidly after weaning (Dusza et al., 1981; Rojkittikhun et al., 1991) and it is thus probable that the threshold concentration of prolactin is maintained to a great extent via feedback from piglet stimuli e.g. during nursings.

The response of somatostatin to nursings still remains unclear. The somatostatin concentration did not appear to change during nursings in our study (III). Algers et al. (1991) found somatostatin to be negatively correlated with the duration of udder massage prior to milk ejection in pigs. The evidence for an association between somatostatin and milk production is also contradictory and unclear at this point. In our study (III), we did not find any association between somatostatin and body resource use or milk production in sows. Similarly, Deligeorgis et al. (1988) did not find any effect of immunisation against somatostatin on milk yield and offspring growth in sheep, and Farmer et al. (1992) did not find any effect of somatostatin immunisation on milk composition in sows. Sow metabolic profiles also appeared unaltered by immunisation against somatostatin, as reported by Farmer et al. (1991). On the other hand, in rats and goats passive immunisation against somatostatin directly improved milk yield (Sun et al., 1997). Considering the results of our

study (III) and the studies by Farmer et al. (1991, 1992) there is to our knowledge so far not any evidence supporting the hypothesis that somatostatin concentrations may be closely related to milk production in sows.

6.8 Oxytocin, prolactin and maternal behaviour

Oxytocin is known to induce general maternal behaviour in at least rodents (for a review see Argiolas and Gessa, 1991) and prolactin also influences nursing behaviour in sows and maternal responsiveness in rodents positively (Bridges et al., 1990; McCarthy et al., 1994; Farmer et al., 1999). We reported that prolactin tended to correlate with nursing duration (II); but we did not find any evidence for an association between prolactin and positive piglet-directed behaviour (III). The positive correlation between non-nursing oxytocin concentration and percentage of sow-terminated nursings suggests a connection between piglet-directed behaviour by the sow and oxytocin concentrations. Sows that often terminated nursings, thereby not allowing the piglets to determine the length of the postmassage period, had higher non-nursing oxytocin concentrations. This result was unexpected and gave rise to speculation, leading to questions such as: a) Is terminating a high proportion of nursings a strategy used by sows with high milk output to save resources for future reproduction? And b) Do well-fed piglets massage less intensively, thus signalling to their dam that there is no urgent need for further milk, as suggested by Špinková and Algiers (1995)?

6.9 Metabolic state during lactation and postweaning reproductive success

The sows could be divided into 2 biologically meaningful groups based on their metabolic pattern during the last 3 weeks of lactation (IV), even though the feeding was similar in both groups and neither litter statistics nor sow weight at parturition differed significantly. Although these two metabolic groups also were apparent after weaning, the groups did not differ in their reproductive functions; we reported similar LH and E₂ concentrations and fertility measures. Only the duration between the onset of oestrus and 1st ovulation tended to be longer in the high- compared to the low-NEFA group. In an earlier study employing a design similar that in IV, Hultèn et al. (1993) also did not find any apparent connection between metabolic status during early lacta-

tion and weaning to oestrus interval. On the other hand, in studies using feeding manipulations, indirect indications of an interaction between metabolic state and postweaning reproductive success have been reported (Reese et al., 1982; Kirkwood et al., 1987; Baidoo et al., 1992b). It is possible that the feeding regime in the present study (near-to ad libitum) prevented energy deficiency severe enough to have detrimental effects on reproductive functions, even when sows were nursing large litters. This is likely, since the rather low urea concentrations indicated that sows did not have to metabolise large amounts of their protein reserves (II).

6.10 Nursing behaviour and postweaning reproductive success

Suckling is the main factor responsible for lactational anoestrus in sows, and nursing frequency has been suggested to be important in this context (Stevenson et al., 1981; De Rensis et al., 1993). In contrast to the findings by Rojkhittikhun et al. (1993), we did not find any evidence for nursing frequency being associated to reproductive functions. Instead, we found that total nursing duration appeared to be related to the reproductive endocrinology of sows (V). Sows with long average nursing duration had significantly lower concentrations of LH during lactation and higher levels of E_2 on the day after weaning. The frequency of LH peaks was also numerically lower in sows with long nursing duration. In addition, postweaning reproductive functions appeared to be negatively related to nursing duration, although the results reported in V are non-significant, i.e. the interval from weaning to 1st oestrus was numerically longer and the ovulation rate lower in sows with long nursing duration.

Long nursing duration appears to be correlated with a stronger inhibitory effect on reproductive functions during and after lactation. We did not find any evidence for nursing duration to be a crucial variable influencing piglet growth (I). Therefore, it can be speculated, bearing in mind the restrictions of the present study (e.g. not allowing for speculations on causal relationships), that there need not be a conflict between good maternal behaviour and postweaning reproductive success.



7. Conclusions

1. Sow nursing-related behaviour does change with proceeding lactation and aspects of an ongoing weaning process can already be seen during the first weeks of lactation as decreased nursing duration and increased avoidance of udder stimulation.

2. Nursing behaviour is not merely a randomly influenced characteristic, but individual sows also differ in their behaviour and the behaviour shows repeatability from day to day, at least within one lactation.

3. The demand on the sow to produce milk (measured as piglet weight gain) is higher during week 3 of lactation than during week 1 and the energy usage cannot fully be compensated for by feed intake. This is reflected as a higher level of catabolism in the sow during the later stage of lactation.

4. Nursing behaviour appears to be linked to the metabolism of the sow via interactions with hormones involved in metabolic functions, i.e. insulin and prolactin.

5. A high nursing frequency is associated with increased piglet weight gain also when sows are not experimentally manipulated. The effect has a similar magnitude throughout lactation.

6. Sows differ in their metabolic state and milk production; those that have low mortality in their litters switch to a high catabolic state early in lactation. Later in lactation, when the demand for milk production peaks (week 3), high litter weight gain is associated with high NEFA concentrations.

7. The role of oxytocin is more important for milk production than merely

serving as an all-or-nothing function in triggering milk ejections. High concentrations of oxytocin are associated with a high catabolic state of the sow and high piglet weight gain.

8. Even though sows fed similarly and nursing similar-sized litters have different metabolic strategies during lactation, this appears not to be related to the postweaning reproductive success in multiparous sows, at least not when sows are fed on near-ad libitum basis.

9. The amount of udder stimuli provided by the piglets (measured as total nursing duration) is negatively associated to reproductive endocrinology and possibly to postweaning reproductive success of sows.



Acknowledgements

This project was performed as a part of the Nordic NKJ-project ‘Maternal behaviour of sows, with focus on genetics, physiology and social environment’ and was carried out in co-operation between the University of Helsinki and at the Swedish University of Agricultural Sciences (SLU). The parts involved include the Department of Clinical Veterinary Sciences, Section for Animal Hygiene at the University of Helsinki, the Department of Animal Environment and Health, the Department of Animal Nutrition and Management and the Department of Obstetrics and Gynaecology at SLU. As several institutes were involved, also a large number of people contributed to the success of the project. I would like to thank everybody who has helped me and motivated me since the project began in 1998. I wish to express my special gratitude to the following:

My main supervisor Bo Algiers for all his encouragement and support and for always showing interest in my thoughts and ideas. His enthusiasm and his insights into the subject have been extremely valuable for my own motivation.

My co-supervisor and professor Hannu Saloniemi for getting me involved in the project in the first place, for believing in me from the very beginning and for helping me solve all kinds of economical and practical problems during these years.

My co-supervisor and co-worker Margareta Rundgren. Her enthusiasm and unlimited storage of knowledge and ideas made the practical performance of the experiment unbelievably fun and interesting. During my stay in Sweden and during all the long hours with the sows I learnt more about sows, pigs, ethology in general and animals in general from her than what any book could ever tell me.

My co-supervisor Marek Špinka, who got involved in the project half-way-through. His positively critical views and comments helped me raise the standard of both the work and of my own knowledge to a level I would never have reached without him.

The pre-examiners, Dan Weary and Beat Wechsler, for their extremely valuable comments on the manuscript of this thesis.

My co-worker Fredrik Hultén, for his help with the sows, for caring for their health, for his involvement in the project in general and for all the interesting discussions we had by the centrifuge during days of blood-sampling.

My co-authors Kerstin Uvnäs-Moberg, Milan Tománek and Peter Krejčí for introducing me to the field of hormonal assays and for their helpfulness. I would also like to thank everybody else, who has been involved in analysing the blood samples, especially Anna-Greta Haglund, for helping me understand the metabolite assays.

Bengt Petterson, for excellent care of our sows and their litters. Working with him was always fun and his support was very important for me during my stays in Sweden.

Peter Lövendahl, Hannu Rita and Aki Niemi for introducing me to the fascinating world of statistics and especially to our “home-statistician” Christian Schnier, who has also been the source of a great deal of good discussions and personal support.

For motivating discussions, good ideas and personal support I owe my very special thanks to the small but enthusiastic group that has been working within applied ethology at the University of Helsinki during these years: Laura Hänninen, Emmi Manninen, Satu Raussi, Susanna Ahlström, Helena Hepola, Anu Katainen, Marianna Norring and Jutta Vierto.

Everybody in the Swine research-group, for introducing me to different fields of swine research.

All the rest of the staff at the Section of Animal Hygiene, especially Ilkka Saastamoinen, for extremely valuable technical support and for the layout-work of this thesis, and Paula Anttila, Suvi Taponen and Taina Kutila for friendly support.

Minna Huovari, Katja Ollikainen and Laura Salonen for helping me analyse the videotapes and for showing interest in the subject, and all the students at SLU, who helped take care of the sows.

I am extremely grateful for being able to work in such good co-operation with a large number of interesting, friendly and fun people from the different Nordic countries. I therefore thank my fellow-PhD-students Karen Thodberg, Katja Grandinsson and Andrew Janczak, and everybody else within the Nordic Network. A very special thanks goes to Lotta Rydhmer for co-ordination of the Nordic project, for practical help and especially for being an infinite source of support during my work.

All the financial supporters: the Finnish Ministry of Agriculture and Forestry, the Swedish Council for Forestry and Agricultural Research, the University of Helsinki, the Finnish Veterinarian fund, the fund for Veterinary Research and the Finnish Society for the Protection of Animals for making this project possible.

My very special thanks go to my family and friends:

To my beloved husband Erik for always supporting me, putting up with me and believing in me, even when I didn't believe in myself anymore,

To my parents for supporting and encouraging me all through my life,

To my brother Björn and his lovely wife Malin, for always welcoming me into their home, thus making my trips to Skara even more worth-while,

To my hairy, four-legged friends Lissu, Rasse, Viiru and Säde for helping me relax and take my mind of work.

And to all my friends from different stages and areas of life, for putting up with this strange pig-person and her bizarre ideas. I would especially like to thank all my fellow-biologists from the University of Helsinki, and everybody at Animalia and Juliana von Wendt's fund for inspiring me to become a scientist and to work with production animals.



References

- Algers, B., 1993. Nursing in pigs: Communicating needs and distributing resources. *J. Anim. Sci.* 71, 2826-2831.
- Algers, B. and Jensen, P., 1985. Communication during suckling in the domestic pig. Effects of continuous noise. *Appl. Anim. Behav. Sci.* 14, 49-56.
- Algers, B., Rojanasthien, S. and Uvnäs-Moberg, K., 1990. The relationship between teat stimulation, oxytocin release and grunting rate in the sow during nursing. *Appl. Anim. Behav. Sci.* 26, 267-276.
- Algers, B. and de Passillé, A.M.B., 1991. En ny syn på smågrisdödligheten. *Svensk Veterinärtidning* 43, 659-663.
- Algers, B., Madej, A., Rojanasthien, S. and Uvnäs-Moberg, K., 1991. Quantitative relationships between suckling-induced teat stimulation and the release of prolactin, gastrin, somatostatin, insulin, glucagon and vasoactive intestinal polypeptide in sows. *Vet. Res. Comm.* 15, 395-407.
- Argiolas, A. and Gessa, G.L., 1991. Central functions of oxytocin. (Review). *Neuroscience & Biobehavioral Reviews* 15, 217-231.
- Armstrong, J.D., Britt, J.H. and Kraeling, R.R., 1986. Effect of restriction of energy during lactation on body condition, energy metabolism, endocrine changes and reproductive performance in primiparous sows. *J. Anim. Sci.* 63, 1915-1925.
- Armstrong, J.D. and Britt, J.H., 1987. Nutritionally-induced anestrus in gilts: metabolic and endocrine changes associated with cessation and resumption of estrus cycles. *J. Anim. Sci.* 65, 508-523.
- Ash, R.W. and Heap, R.B., 1975. Oestrogen, progesterone and corticosteroid concentrations in peripheral plasma of sows during pregnancy, parturition, lactation and after weaning. *J. Endocrinology* 64, 141-154.
- Auldust, D.E., Carlson, D., Morrish, L., Wakeford, C.M. and King, R.H., 2000. The influence of suckling interval on milk production of sows. *J. Anim. Sci.* 78, 2026-2031.
- Baidoo, S.K., Lythgoe, E.S., Kirkwood, R.N., Aherne, F.X. and Foxcroft, G.R., 1992a. Effect of lactation feed intake on endocrine status and metabolite levels in sows. *Can. J. Anim. Sci.* 72, 799-807.

- Baidoo, S.K., Aherne, F.X., Kirkwood, R.N. and Foxcroft, G.R., 1992b. Effect of feed intake during lactation and after weaning on sow reproductive performance. *Can. J. Anim. Sci.* 72, 911-917.
- Ballou, L.U., Bleck, J.L., Bleck, G.T. and Bremel, R.D., 1993. The effects of daily oxytocin injections before and after milking on milk production, milk plasmin and milk composition. *J. Dairy Sci.* 76, 1544-1549.
- Barber, M.C., Clegg, R.A., Finley, E., Vernon, R.G. and Flint, D.J., 1992. The role of growth hormone, prolactin and insulin-like growth factors in the regulation of rat mammary gland and adipose tissue metabolism during lactation. *J. Endocrinology* 135, 195-202.
- Billie, N., Nielsen, N.C., Larsen, J.L. and Svendsen, J., 1974. Prewaning mortality in pigs. 2. The perinatal period. *Nord. Vet. Med.* 26, 294-313.
- Björkstrand, E., Eriksson, M. and Uvnäs-Moberg, K., 1996. Evidence of a peripheral effect of oxytocin on pancreatic hormone release in rats. *Neuroendocrinology* 63, 377-383.
- Bridges, R.S., Numan, M. and Ronsheim, P.M., 1990. Central prolactin infusions stimulate maternal behaviour in steroid-treated, nulliparous female rats. *Proc. National Academy Sci. U.S.* 87, 8003-8007.
- Bäckström, L., 1973. Environment and animal health in piglet production. *Acta Vet. Scand. Suppl.* 41, 240.
- Bäckström, L., Morkoc, A.C., Connor, J., Larson, R. and Price, W., 1984. Clinical study of mastitis-metritis-agalactia in sows in Illinois. *J. American Vet. Med. Ass.* 185, 70-73.
- Bøe, K., 1991. The process of weaning in pigs: when the sow decides. *Appl. Anim. Beh. Sci.* 30, 47-59.
- Bøe, K., 1993. Maternal behaviour of lactating sows in a loose-housing system. *Appl. Anim. Behav. Sci.* 35, 327-338.
- Bøe, K., 1994. Variation in maternal behaviour and production of sows in integrated loose housing systems in Norway. *Appl. Anim. Behav. Sci.* 41, 53-62.
- Castrén, H., Algers, B. and Jensen, P., 1989. Occurrence of unsuccessful sucklings in newborn piglets in a semi-natural environment. *Appl. Anim. Behav. Sci.* 23, 61-73.
- Castrén, H., Algers, B., De Passillé, A.M., Rushen, J. and Uvnäs-Moberg, K., 1993a. Parturient variation in progesterone, prolactin, oxytocin and somatostatin in relation to nest building in sows. *Appl. Anim. Behav. Sci.* 38, 91-102.
- Castrén, H., Algers, B., De Passillé, A.M., Rushen, J. and Uvnäs-Moberg, K., 1993b. Early milk ejection, prolonged parturition and periparturient oxytocin release in the pig. *Anim. Prod.* 57, 465-471.
- Castrén, H., Algers, B., De Passillé, A.M., Rushen, J. and Uvnäs-Moberg, K., 1994. Nest building in sows in relation to hormone release. *Appl. Anim. Behav. Sci.* 40, 74-75.

- Clough, C.E., 1984. An evaluation of the farrowing crate. *Farm Building Progress* 76, 21-26.
- Clutton-Brock, J., 1999. *A Natural History of Domestic Animals*, 2nd ed. University Press. Cambridge.
- Collier, R.J., McNamara, J.P., Wallace, C.R. and Dehoff, M.H., 1984. A review of endocrine regulation of metabolism during lactation: *J. Anim. Sci.* 59, 498-510.
- De Braganca, M.M. and Prunier, A., 1999. Effects of low feed intake and hot environment on plasma profiles of glucose, nonesterified fatty acids, insulin, glucagon, and IGF-I in lactating sows. *Dom. Anim. Endocrinol.* 16, 89-101.
- Deligeorgis, S.G., Rogdakis, E., Mantzios, A., Nikolaon, E., Evangelatos, G. and Sotiriadis-Vlahos, C., 1988. A note of the effect of active immunisation against somatostatin on milk production and growth in sheep. *Anim. Prod.* 46: 304-308.
- De Passillé, A.M.B., Rushen, J. and Pelletier, G., 1988. Sucking behaviour and serum immunoglobulin levels in neonatal piglets. *Anim. Prod.* 47, 447-456.
- De Passillé, A.M.B. and Rushen, J., 1989. Using early suckling behavior and weight gain to identify piglets at risk. *Can. J. Anim. Sci.* 69, 535-544.
- De Passillé, A.M.B., Rushen, J., Foxcroft, G.R., Aherne, F.X. and Schaefer, A., 1993. Performance of young pigs: relationships with periparturient progesterone, prolactin, and insulin of sows. *J. Anim. Sci.* 71, 179-184.
- De Rensis, F., Hunter, M.G. and Foxcroft, G.R., 1993. Suckling-induced inhibition of luteinizing hormone secretion and follicular development in the early postpartum sow. *Biol. Reprod.* 48, 964-969.
- Dubreuil, P., Pelletier, G., Petitclerc, D., Lapierre, H., Couture, Y., Gaudreau, P., Morisset, J. and Brazeau, P., 1990. Influence of growth hormone-releasing factor and(or) thyrotropin-releasing factor on sow blood components, milk composition and piglet performance. *Can. J. Anim. Sci.* 70, 821-832.
- Dusza, L. and Krzymowska, H., 1979. Plasma prolactin concentrations during oestrous cycle in sows. *J. Reprod. Fert.* 76, 519-525.
- Dusza, L., Krzymowska, H., Oksara, S., Czernyiszewicz, J., Kotwica, G., Koziowski, M., Kuznia, S., Czarnocki, J., Debek, J. and Nowicka, R., 1981. The PRL, E₂, T, progesterone, corticoids and T3 estimations in sow's plasma during lactation and some days after weaning. *Advances in Physiol. Sci.* 20, 197-202.
- Dyck, G.W. and Swierstra, E.E., 1987. Causes of piglet death from birth to weaning. *Can. J. Anim. Sci.* 67, 543-547.
- Eckert, R., Randall, D. and Augustine, G., 1988. *Animal Physiology*, 3rd ed. W.H. Freeman and Company. New York.
- Edwards, S.A., Malkin, S.J. and Spechter, H.H., 1986. An analysis of piglet mortality with behavioural observations. *British Society of Animal Production. Winter Meeting*, 17-29

March 1986, Grand Hotel, Scarborough, Paper 126, 2.

Edwards, S.A., Smith, W.J., Fordyce, C. and MacMenemy, F., 1994. An analysis of the causes of piglet mortality in a breeding herd kept outdoors. *Vet. Rec.* 135, 324-327.

Efendic, S., Enzmann, F., Nylén, F., Uvnäs-Wallensten, K. and Lufft, R., 1980. Sulfonylurea (Glibenclamide) enhances somatostatin and inhibits glucagon release induced by arginine. *Acta. Physiol. Scand.* 108, 231-233.

Efendic, S. and Uvnäs-Wallensten, K., 1983. Somatostatin: Physiological significance with emphasis on the pancreas and gastrointestinal tract. *Period Biol.* 85, Suppl. 1, 95-106.

Einarsson, S., Rojkittikhun, T. and Uvnäs-Moberg, K., 1992. Metabolic and reproductive hormones during lactation and the post-weaning period in sows. (Review). *J. Physiol. Pharm.* 43, 207-213.

Ellendorff, F., Forsling, M.L. and Poulain, D.A., 1982. The milk ejection reflex in the pig. *J. Physiol.* 333, 577-594.

Ellendorff, F. and Poulain, D., 1984. A means to assess nursing efficiency in the pig: the study of the milk ejection reflex. *Ann. Rech. Vet.* 15, 271-274.

Farmer, C., Dubreuil, P., Pelletier, G., Peticlarc, D., Gaudreau, P. and Brazeau, P., 1991. Effects of active immunization against somatostatin (SRIF) and/or injections of growth hormone-releasing factor (GRF) during gestation on hormonal and metabolic profiles in sows. *Domest. Anim. Endocrinol.* 8, 415-422.

Farmer, C. and Brazeau, P., 1992. Colostrum and milk composition of sows immunised against somatostatin and its carrier protein. *Can. J. Anim. Sci.* 72, 177-180.

Farmer, C., Robert, S. and Rushen, J., 1998. Bromocriptine given orally to periparturient or lactating sows inhibits milk production. *J. Anim. Sci.* 76, 750-757.

Farmer, C., Sorensen, M.T., Robert, S. and Petitclerc, D., 1999. Administering exogenous porcine prolactin to lactating sows: Milk yield, mammary gland composition, and endocrine and behavioral responses. *J. Anim. Sci.* 77, 1851-1859.

Farmer, C., 2001. The role of prolactin for mammaryogenesis and galactopoiesis in swine. *Livest. Prod. Sci.* 70, 105-113.

Flint, D.J., 1982. Regulation of insulin receptors by prolactin in lactating rat mammary gland. *J. Endocrinol.* 93, 279-285.

Flint, D.J., 1985. Role of insulin and the insulin receptor in nutrient partitioning between the mammary gland and adipose tissue. *Biochemical Society Transactions* 13, 828-829.

Flint, D.J., 1995. Regulation of milk secretion and composition by growth hormone and prolactin. In: Wilde, C.J., Peaker, M. (Eds.), *Intercellular signalling in the mammary gland*. Plenum Press, New York, pp. 131-140.

Flint, D.J., Sinnott, S.P., Clegg, R.A., and Vernon, R.G., 1979. Role of insulin receptors in the

changing metabolism of adipose tissue during pregnancy and lactation in the rat. *Biochemical J., Cellular Aspects* 182, 421-427.

Forsberg, M., Tagle, R., Madej, A., Molina, J.R. and Carlsson, M.-A., 1993. Radioimmunoassay of bovine, ovine and porcine luteinizing hormone with a monoclonal antibody and a human tracer. *Acta. Vet. Scand.* 34, 255-262.

Fraser, D., 1977. Some behavioural aspects of milk ejection failure by sows. *Br. Vet. J.* 133, 126-133.

Fraser, D., 1980. A review of the behavioural mechanism of milk ejection of the domestic pig. *Appl. Anim. Ethology* 6, 247-255.

Fraser, D., Phillips, P.A. and Thompson, B.K., 1997. Farrowing behaviour and stillbirth in two environments: an evaluation of the restraint-stillbirth hypothesis. *Appl. Anim. Behav. Sci.*, 55, 51-66.

Garssen, G.J., Welling, A.M.A.W. and Spencer, G.S.G. 1987. Active immunisation against somatostatin increases milk yield in goats. *Netherlands J. Agricultural Sci.* 35, 84-86.

Glastonbury, J.R.W., 1976. A survey of preweaning mortality in the pig. *Australian Vet. J.* 52, 272-276.

Glastonbury, J.R.W., 1977. Preweaning mortality in the pig. The prevalence of various causes of preweaning mortality and the importance of some contributory factors. *Australian Vet. J.* 53, 315-318.

Goodman, G.T. and Grosvenor, C.E., 1983. Neuroendocrine control of the milk ejection reflex. (Review). *J. Dairy Sci.* 66, 2226-2235.

Götz, M., 1991. Changes in nursing and suckling behavior of sows and their piglets in farrowing crates. *Appl. Anim. Beh. Sci.* 31, 271-276.

Herpin, P., Le Dividich, J. and Amaral, N., 1993. Effect of selection for lean tissue growth on body composition and physiological state of the pig at birth. *J. Anim. Sci.* 71, 2645-2653.

Hultén, F., Neil, M., Einarsson, S. and Håkansson, J., 1993. Energy metabolism during late gestation and lactation in multiparous sows in relation to backfat thickness and the interval from weaning to first oestrus. *Acta Vet. Scand.* 34, 9-20.

Illmann, G. and Madlafousek, J., 1995. Occurrence and characteristics of unsuccessful nursings in minipigs during the first week of life. *Appl. Anim. Behav. Sci.* 44, 9-18.

Jarvis, S., Lawrence, A.B., McLean, K.A., Deans, L.A., Chirnside, J. and Calvert, S.K., 1997. The effect of environment on behavioural activity, ACTH, beta-endorphin and cortisol in pre-farrowing gilts. *Anim. Sci.* 65, 465-472.

Jensen, P., 1986. Observations on the maternal behaviour of free-ranging domestic pigs. *Appl. Anim. Behav. Sci.* 16, 131-142.

Jensen, P., 1988. Maternal behaviour and mother-young interactions during lactation in free-ranging domestic pigs. *Appl. Anim. Behav. Sci.* 20, 297-308.

Jensen, P. and Recen, B., 1989. When to wean - observations from free-ranging domestic pigs. *Appl. Anim. Behav. Sci.* 23, 49-60.

Johnson, R.K., Nielsen, M.K. and Casey, D.S., 1999. Responses in ovulation rate, embryonal survival, and litter traits to 14 generations of selection to increase litter size. *J. Anim. Sci.* 77, 541-557.

Kenison, D.C., Schelling, G.T., Byers, F.M. and Greene, L.W., 1987. Lactational performance and growth hormone secretion in dairy goats immunized against somatostatin. *J. Dairy. Sci.* 70, Suppl. 1: 177.

Kerr, J.C. and Cameron, N.D., 1996. Responses in gilt post-farrowing traits and pre-weaning piglet growth to divergent selection for components of efficient lean growth rate. *Anim. Sci.* 63, 523-531.

King, R.H. and Williams, I.H., 1984. The effect of nutrition on the reproductive performance of first-litter sows. 1. Feeding level during lactation, and between weaning and mating. *Anim. Prod.* 38, 241-247.

Kirkwood, R.N., Baidoo, S.K., Aherne, F.X. and Sather, A.P., 1987. The influence of feeding level during lactation on the occurrence and endocrinology of the postweaning estrus in sows. *Can. J. Anim. Sci.* 67, 405-415.

Klocek, C., Koczanowski, J., Migdal, W. and Nowicki, J., 2000. Parturition behaviour and course of farrowing of sows housed with and without freedom of movement. *Advances in Agricultural Sci.* 7, 25-28.

Knol, E.F., 2001. Genetic aspects of piglet survival. PhD Thesis. Wageningen University, The Netherlands.

Kraetzl, W.D., Zimmer, C., Schneider, D. and Schams, D., 1998. Secretion pattern of growth hormone, prolactin, insulin and insulin-like growth factor-1 in the periparturient sow depending on the metabolic state during lactation. *Anim. Sci.* 67, 339-347.

Kunavongkrit, A., 1984. Clinical and endocrinological studies in primiparous post partum sows. Effects of lactation length and litter size. *Acta Vet. Scand.* 25, 260-279.

Lawrence, A.B., Petherick, J.C., McLean, K.A., Deans, L.A., Chirnside, J., Vaughan, A., Clutton, E. and Terlouw, E.M.C., 1994. The effect of environment on behaviour, plasma cortisol and prolactin in parturient sows. *Appl. Anim. Behav. Sci.* 39, 313-330.

Lawrence, A.B., Petherick, J.C., McLean, K.A., Deans, L.A., Chirnside, J., Vaughan, A., Gilbert, C.L., Forsling, M.L and Russell, J.A., 1995. The effects of chronic environmental stress on parturition and oxytocin and vasopressin secretion in the pig. *Anim. Reprod. Sci.* 38, 251-264.

Le Cozler, Y., David, C., Beaumal, V., Johansen, S. and Dourmand, J.Y., 1998. Effects of

feeding level during rearing on performance of Large White gilts. Part 2: effect on metabolite profiles during gestation and lactation, and glucose tolerance. *Reprod. Nutr. Develop.* 38, 377-390.

Marchant, J.N. and Broom, D.M., 1996. Factors affecting posture-changing in loose-housed and confined gestating sows. *Anim. Sci.* 63, 477-485.

McCarthy, M.M., Curran, G.H. and Siegel, H.I., 1994. Evidence for the involvement of prolactin in the maternal behaviour of the hamster. *Phys. Behav.* 55, 181-184.

McKay, R.M., 1993. Prewaning losses of piglets as a result of index selection for reduced backfat thickness and increased growth rate. *Can. J. Anim. Sci.* 73, 437-442.

Meunier-Salaun, M.C., Gort, F., Prunier, A. and Schouten, W.P.G., 1991. Behavioural patterns and progesterone, cortisol and prolactin levels around parturition in European (Large-White) and Chinese (Meishan) sows. *Appl. Anim. Behav. Sci.* 31, 43-59.

Mulloy, A.L. and Malven, P.V., 1979. Relationships between concentrations of porcine prolactin in blood serum and milk of lactating sows. *J. Anim. Sci.* 48, 876-881.

Nurmisto, U. (ed.), 1987. *Maatalouden rakennusoppi*. Kirjayhtymä, Helsinki.

Quesnel, H. and Prunier, A., 1995. Endocrine bases of lactational anoestrus in the sow. *Reprod. Nutr. Develop.* 35, 395-414.

Quesnel, H., Pasquier, A., Mounier, A.M., Louveau, I. and Prunier, A., 1998a. Influence of feed restriction in primiparous lactating sows on body condition and metabolic parameters. *Reprod. Nutr. Develop.* 38, 261-274.

Quesnel H., Pasquier, A., Mounier, A.M. and Prunier, A., 1998b. Influence of feed restriction during lactation on gonadotropic hormones and ovarian development in primiparous sows. *J. Anim. Sci.* 76, 856-863.

Ranta, E., Rita, H. and Kouki, J., 1994. *Biometria. Tilastotiedettä ekologeille*. 5th ed. Yliopistopaino, Helsinki.

Rautala, H., 2002, *Sikojen terveystarkkailu*. Sika 3, 9.

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

Rodriguez, H. and Kunavongkrit, A., 1983. Chronical venous catheterization for frequent blood sampling in unrestrained pigs. *Acta Vet. Scand.*, 24, 318-320.

Rojkittikhun, T., Uvnäs-Moberg, K., Einarsson, S. and Lundeheim, N., 1991. Effect of weaning on plasma levels of prolactin, oxytocin, insulin, glucagon, glucose, gastrin and somatostatin in sows. *Acta Physiol. Scand.* 141, 295-303.

Rojkittikhun, T., Einarsson, S., Edqvist, L.E., Uvnäs-Moberg, K. and Lundeheim, N., 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. Series A* 39, 426-432.

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

Rojkittikhun, T., Einarsson, S., Uvnäs-Moberg, K., Lundeheim, N. and Madej, A., 1993b. Patterns of release of oxytocin, prolactin, insulin and LH in lactating sows, studied using continuous blood collection technique. *J. Vet. Med. Series A* 40, 412-421.

Rushen, J. and Fraser, D., 1989. Nutritive and nonnutritive sucking and the temporal organization of the suckling behavior of domestic piglets. *Develop. Psychobiology* 22, 789-801.

Rushen, J., Foxcroft, G. and de Passillé, A.M.B., 1993. Nursing-induced changes in pain sensitivity, prolactin, and somatotropin in the pig. *Physiol. Behav.* 53, 265-270.

SAS Institute, 1997. SAS/STAT Software: Changes and enhancements through Release 6.12, 1st edn., SAS Institute Inc., Cary, NC.

Sinclair, A.G., Edwards, S.A., Hoste, S. and McCartney, A., 1998. Evaluation of the influence of maternal and piglet breed differences on behaviour and production of Meishan synthetic and European White breeds during lactation. *Anim. Sci.* 66, 423-430.

Spincer, J.J., Rook, J.A.F. and Towers, K.G., 1969. The uptake of plasma constituents by the mammary gland of the sow. *Biochem. J.* 111: 727-735.

Špinka, M. and Algers, B., 1995. Functional view on udder massage after milk let-down in pigs. *Appl. Anim. Behav. Sci.* 43, 197-212.

Špinka, M., Illmann, G., Algers, B. and Štetková, Z., 1997. The role of nursing frequency in milk production in domestic pigs. *J. Anim. Sci.* 75, 1223-1228.

Špinka, M., Illmann, G., Štetková, Z., Krejčí, P., Tománek, M., Sedlák, L. and Lidický, Z., 1999. Prolactin and insulin levels in lactating sows in relation to nursing frequency. *Dom. Anim. Endocr.* 17, 53-64.

Špinka, M., Stéhulová, I., Zachacová, J., Maletínská, J. and Illmann, G., 2002. Nursing behaviour and nursing vocalisations in domestic sows: repeatability and relationship with maternal investment. *Behav.* 139, 1077-1097.

SPSS Inc., 1998. SPSS Base 8.0 for Windows User's Guide. SPSS Inc. Chicago. IL.

Sternberg, K., 2002. Sikatarkkailun tuloksia vuodelta 2001. Pilkahdus paremmasta. *Sika* 3, 4-7.

Sterning, M., Rydhmer, L., Eliasson, L., Einarsson, S. and 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.

Stevenson, J.S. and Britt, J.H., 1980. Luteinizing hormone, total estrogens and progesterone secretion during lactation and after weaning in sows. *Theriogenology* 14, 453-462.

Stevenson, J.S., Cox, N.M. and Britt, J.H., 1981. Role of the ovary in controlling luteinizing hormone, follicle stimulating hormone, and prolactin secretion during and after lactation in pigs. *Biology of Reproduction*. 24, 341-353.

Stock, S. and Uvnäs-Moberg, K., 1985. Oxytocin infusions increase plasma level of insulin and VIP but not of gastrin in conscious dogs. *Acta Physiol. Scand.* 125, 205-210.

Sun, S.S., Jang, K., Kuk, K., Myung, K.H. and Choi, Y.J., 1997. The effects of somatostatin passive immunization on milk yield, plasma hormone and metabolite concentrations in rats. *Asian Australasian J. Anim. Sci.* 10, 324-328.

Suva, J., Caisova, D. and Stajner, A., 1980. Modification of fat and carbohydrate metabolism by neurohypophysal hormones. III. Effect of oxytocin on non-esterified fatty acid, glucose, triglyceride and cholesterol levels in rat serum. *Endokrinologie* 76, 333-339.

Thodberg, K., 2001. Individual variation in maternal behaviour of gilts and sows – effects of environment, experience and reactivity. PhD Thesis. The Royal Veterinary and Agricultural University and Department of Animal Science and Animal Health, Denmark.

Thodberg, K., Jensen, K.H. and Herskin, M.S., 2002. Nest building and farrowing in sows: relation to the reaction pattern during stress, farrowing environment and experience. *Appl. Anim. Behav. Sci.* 77, 21-42.

Thompson, B.K. and Fraser, D., 1988. Variation in piglet weights: weight gains in the first days after birth and their relationship with later performance. *Can. J. Anim. Sci.* 68, 581-590.

Toner, M.S., King, R.H., Dunshea, F.R., Dove, H. and Atwood, C.S., 1996. The effect of exogenous somatotropin on lactation performance of first-litter sows. *J. Anim. Sci.* 74, 167-172.

Tsuma, V.T., Einarsson, S., Madej, A. and Lundeheim, N., 1995. Hormone profiles around weaning in cyclic and anoestrus sows. *J. Vet. Med. Assoc.* 42, 153-163.

Uvnäs-Moberg, K., Eriksson, M., Blomquist, L.E., Kunavongkrit, A. and Einarsson, S., 1984. Influence of suckling and feeding on insulin, gastrin, somatostatin and VIP levels in peripheral venous blood of lactating sows. *Acta Physiol. Scand.* 121, 31-38.

Uvnäs-Moberg, K., Johansson, B., Lupoli, B. and Svennersten-Sjaunja, K., 2001. Oxytocin facilitates behavioural, metabolic and physiological adaptations during lactation. *Appl. Anim. Behav. Sci.* 72, 225-234.

Van der Steen, H.A.M., Schaeffer, L.R., Jong, H.D. and Groot, P.D., 1988. Aggressive behavior of sows at parturition. *J. Anim. Sci.* 66, 271-279.

Vangen, O., Holm, B., Rossly, T., Vasbotten, M., Valros, A. and Rydhmer, L., 2002. Genetic variation in maternal behaviour of sows. 7th World Congr. Genet. Appl. Livest. Prod. Montpellier, France.

Varley, M.A., Foxcroft, G.R., Cole, D.J.A. and Weir, B.J., 1989. Endocrinology of the lactating and weaned sow: Control of pig reproduction. *Proceedings of the Third International*

Conference on Pig Reproduction, held at Sutton Bonington, UK, Suppl. 40, 47-61.

Verheijen, C., 2001. Genetic and biological aspects of mothering ability in sows. Master's Thesis. Wageningen University, The Netherlands.

Weary, D.M., Pajor, E.A., Thompson, B.K. and Fraser, D., 1996. Risky behaviour by piglets: a trade off between feeding and risk of mortality by maternal crushing? *Anim. Behav.* 51, 619-624.

Wechsler, B. and Brodmann, N., 1996. The synchronization of nursing bouts in group-housed sows. *Appl. Anim. Behav. Sci.* 47, 191-199.

Watson, T.S. and Bertram, J.M., 1980. A comparison of incomplete nursing in the sow in two environments. *Anim. Prod.* 30, 105-114.

Widowski, T.M., Curtis, S.E., Dziuk, P.J., Wagner, W.C. and Sherwood, O.D., 1990. Behavioural and endocrine responses of sows to prostaglandin $F_2\alpha$ and chloroprostenol. *Biol. Reprod.* 42, 290-297.

Widström, A.M., Winberg, J., Werner, S., Svensson, K., Posloncec, B. and Uvnäs-Moberg, K., 1988. Breast feeding-induced effects on plasma gastrin and somatostatin levels and their correlation with milk yield in lactating females. *Early Human Develop.* 16, 293-301.

Zak, L.J., Cosgrove, J.R., Agerna, F.X. and Foxcroft, G.R., 1997. Pattern of feed intake and associated metabolic and endocrine changes differentially affect postweaning fertility in primiparous lactating sows. *J. Anim. Sci.* 75, 208-216.

Zak, L.J., Williams, I.H., Foxcroft, G.R., Pluske, J.R., Cegielski, A.C., Clowes, E.J. and Aherne, F.X., 1998. Feeding lactating primiparous sows to establish three divergent metabolic states: I. Associated endocrine changes and postweaning reproductive performance. *J. Anim. Sci.* 76, 1145-1153.