Effects of nutrition on pregnant and lactating sows

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It has been suggested that the long-term reproduction of the sow is best served by minimizing weight and fat loss in lactation. Such a strategy would require only a minimal restoration of weight in the following pregnancy, which would be beneficial, since the greater feed intake and weight gain in pregnancy, the greater the weight loss in lactation. Feeding *ad libitum* should be practised during lactation while gestation feed intake must be held low. A relationship between feed intake and embryo survival has been demonstrated in several studies, but the data are sometimes difficult to interpret. High energy feeding during the premating period and during early pregnancy, however, are often associated with increased embryo mortality. A short-term starvation in lactation decreased prolactin to post-weaning concentrations, and insulin and glucose to very low concentrations. Prolactin increased very rapidly after refeeding indicating that a neural mechanism might be involved. The increasing levels of cholecystokinin after refeeding and the neural reflex triggered might be related to this increase in prolactin. No changes in LH release were observed during the periods of starvation or refeeding. The catabolic rate during the first week of lactation is higher in sows with higher backfat thickness than in late gestation. As lactation progresses a more balanced metabolism is achieved regardless of backfat thickness before parturition. High-weight-loss primiparous sows need a longer recovery period from their negative energy balance during lactation than do low-weight-loss primiparous sows or multiparous sows. Several investigations have demonstrated that sows losing excessive amounts of body weight have extended weaning to oestrous intervals and an increase in anoestrus. Sows with low body-weight loss during lactation have higher plasma insulin and lower cortisol around weaning than do sows with high body-weight loss. What remains undefined is the degree of weight or condition loss below which an extension in the remating interval will occur and the level of dietary energy intake required to prevent this extension.

Introduction

It has been known for a long time that there is a relationship between nutrition and reproduction. However, the physiological mechanisms by which intake of energy affects reproductive performance of sows have not been clearly determined. The energy and protein substrates that are necessary for the physiological processes are derived from the diet and the body reserves. When dietary supply exceeds the demand of these processes, substrates are stored as fat, glycogen or protein. However, when the demand exceeds dietary intake, these reserves are mobilized. It has been suggested that the long-term reproduction of sows is best served by minimizing weight and fat loss in lactation. Such a strategy would require only a minimal restoration of weight in the following pregnancy which would be beneficial, since the greater feed intake and weight gain in pregnancy, the greater the potential weight loss in lactation.
The purpose of this paper is to briefly describe (1) the influence of nutrition in pregnancy, (2) the relationship between feed intake during pregnancy and lactation, (3) metabolism during late gestation and lactation, (4) feeding-related endocrine changes during lactation and (5) lactation-associated weight loss, metabolic and reproductive hormones and the weaning to oestrous interval in sows.

Influence of Nutrition in Early Pregnancy

There is no clear evidence about the influence of nutrition on conception rate. Den Hartog and van Kempen (1980) reviewed the results of 26 experiments with high and low feeding during the pubertal period, during the oestrous cycle or during both periods in gilts and found no significant differences in conception rates. An adverse effect of large body weight losses during lactation on conception rate was reported by Hardy and Lodge (1969) but this was not confirmed in later studies (for example Reese et al., 1982b; King et al., 1984; King and Williams, 1984a).

Nutrition in early pregnancy has been extensively reviewed (for example Anderson and Melampy, 1972; den Hartog and van Kempen, 1980). In some experiments a relationship has been shown between feed intake and embryo survival, but the data are sometimes difficult to interpret because of the variation in duration of treatment (Cole, 1982). Improved embryo survival with gilts given lower feed levels have been reported (for example Dutt and Chaney, 1968; Dyck and Strain, 1980). They demonstrated a benefit when feed intake was reduced from the day of mating to day 10 of pregnancy (daily feed intake of 1.25 or 1.5 kg). A high level of feeding during rearing is associated with an increase in ovulation rate at first, second or third oestrus and with a reduction in embryo survival during early gestation (den Hartog and van Kempen, 1980; den Hartog, 1984). High energy feeding during the premating period is also associated with a reduced embryo survival during early gestation in gilts. The reason for this is unclear, but gilts with high energy intakes also had an increased ovulation rate and this _per se_ may lead to increased embryo mortality. Toplis et al. (1983), however, failed to confirm an effect of high energy intake on early embryo survival. They suggested that since the various nutritional regimens in earlier reported studies were usually implemented at or very soon after mating, an increase in ovulation rate may have occurred; and, as described above, increased ovulation rates could then be associated with increased embryo mortality.

Pharazyn et al. (1991) reported that feeding gilts with two levels of energy and protein from days 3 to 15 of gestation had no effect on plasma progesterone in early pregnancy or embryo survival to day 28. However, overall plasma progesterone concentrations on day 3 were positively related to embryo survival and inversely related to variance in survival. They therefore proposed that changes in circulating progesterone in the immediate period after ovulation may be of greater importance in determining embryo survival than are progesterone concentrations later in gestation. In trials in which embryo survival is decreased, the effect may be mediated by a reduction in plasma progesterone. Both increased feed and protein in early pregnancy have been shown to influence plasma progesterone (Jordan and Swanson, 1979; Dyck et al., 1980; Parr et al., 1993). Parr et al. (1993) showed that high feed levels after mating reduce peripheral progesterone concentrations and increase embryonic mortality. They also tried to correct this with exogenous progesterone and their preliminary results are very promising. Grandhi (1988) reported reduced concentrations of progesterone in plasma and embryo survival in gilts fed diets supplemented with fat during gestation. The mechanism underlying the reduction in plasma progesterone associated with increased feed or energy intake during early gestation is still unknown. Different hypotheses have been presented but are still controversial. Hughes and Pearce (1989) suggested that any nutritional regimen that causes rapid body weight and condition gains in gilts/sows during early gestation is likely to result in reduced embryo survival, as a consequence of increased hepatic blood flow increasing the metabolic clearance rate of progesterone. This hypothesis was supported by data from a study in ovariectomized nonpregnant gilts (Symonds and Prime, 1988). The portal blood flow and the metabolic clearance of progesterone from plasma (MCR) increased significantly when the food intake was increased (Symonds and Prime, 1988).

Several studies have also been performed to elucidate the effect of feeding during lactation on subsequent embryo survival in sows. King and Williams (1984a,b) found that low lactation, dietary
energy or protein intake did not affect embryo survival. Hughes et al. (1984) and King et al. (1984) found lower embryo survival in sows fed 3 kg day\(^{-1}\) compared with sows fed 7 kg day\(^{-1}\), despite the fact that the ovulation rate was approximately the same in the two groups of sows. An important question is whether a minimum backfat level must be achieved, rather than a minimum backfat depletion, before embryo survival is compromised (Aheme and Kirkwood, 1985). According to Cole (1990), it is generally recognized that it is more likely to be the depletion of tissues that is important rather than weight loss per se and that the relationship between changes in body weight and changes in fat is not good as sows can gain weight but lose fat at the same time.

In sows having excessive weight and fat losses in lactation, it is again possible that an increased hepatic blood flow after weaning increases the metabolic clearance rate of plasma progesterone and thereby reduces the plasma progesterone (Aheme and Kirkwood, 1985). It has also been suggested that the effects of low lactation feeding on embryo survival are the result of suboptimal LH release at the oestrus after weaning, resulting in inadequate luteinization of the corpora lutea, with concomitant low plasma progesterone in early pregnancy. Further support for this hypothesis comes from a study demonstrating that injection of GnRH at the oestrus after weaning improved embryo survival and increased progesterone concentrations in early gestation in sows fed low levels during lactation (Kirkwood et al., 1987). It is suggested that further studies are needed in this area, in particular on the link between endocrine status of sows and nutrient intake, body weight and composition, and rates of tissue change.

**Influence of Nutrition in Mid- and Late Pregnancy**

The response to energy intake in pregnancy is generally reflected in the response to total feed intake (Cole, 1982). The sow needs food to meet the demands of the developing fetuses and to achieve some weight gain. During pregnancy, maintenance represents 75–85% of the total requirements and is affected by environmental temperature and activity of the animals (Noblet et al., 1990). In addition to the requirements for total uterine gain, the daily metabolizable energy (ME) requirements during pregnancy depend on the amount and composition of maternal weight gain and on the previous lactation body weight loss. Large weight gains in pregnancy are not considered desirable in maintaining optimum weight change and body condition in the long-term reproduction of sows. The level of energy intake during gestation appears to have little effect on litter size (e.g. Pond, 1973; Etienne, 1979; Gatel et al., 1987). However, birth weight may be reduced with energy restriction.

Few reports are available in which sufficient numbers of sows were used to compare reproductive performance in which different amounts of energy were used to compare reproductive performance when different amounts of energy were fed throughout consecutive gestations. In a comprehensive study (Young et al., 1990), 187 pregnant gilts were fed three gestation energy levels 22.2, 29.2 and 36.2 MJ digestible energy (DE) per day for four parities to assess the effect of gestation energy level on reproductive performance. All sows were fed the same lactation diet to appetite twice per day. Gestation energy level did not have a consistent effect on the number of piglets per litter. There was a small linear increase in piglet birth weight as gestation energy level increased. Weight and backfat thickness of sows tended to change with the level of food intake. As in similar studies, it was demonstrated that sows that ate more at gestation tended to eat less in lactation. Fewer sows that were fed the low gestation energy level completed parities three and four and the major reason for sow removal was that sows were not pregnant at the expected time of farrowing.

Several studies indicate that piglet birth weight is moderately correlated with sow feed intake during gestation. Dietary treatments that increase piglet glycogen or fat stores during late gestation are beneficial for improving neonatal survival (Britt, 1986). Severe restriction of energy or protein intake during mid- or late gestation reduces piglet birth weight, but not embryo survival rate (Pond, 1973; Shields et al., 1985; Pond et al., 1986). The effect of prolonged starvation during either the middle third or last third of gestation closely parallels the effects observed during dietary energy restriction (Anderson et al., 1979; Hard and Anderson, 1979). It is suggested that the feed level of pregnant sows after the first 2–4 weeks of gestation has little effect on litter size.
Relationship Between Feed Intake During Pregnancy and Lactation

There is a close relationship between feed intake in pregnancy and feed intake in lactation. It was convincingly demonstrated by Salmon-Legagneur and Rerat (1962) that a high feed intake in pregnancy results in a lower feed intake in lactation, due at least in part to a reduced appetite in lactation. Mullan and Williams (1989) showed that when the level of body reserves was increased before farrowing, sows had a lower voluntary feed intake during lactation than those animals that farrowed with a low level of body reserves. It is also well established that the greater the weight gain and level of backfat deposition during gestation, the greater will be the weight and backfat depletion during the subsequent lactation (e.g. Brooks and Smith, 1980; O'Grady, 1980; Young et al., 1990). The long-term reproduction of sows is best served by minimizing weight and fat loss in lactation (Cole, 1982). Such a strategy would require only a minimal restoration of weight in the following pregnancy. The results from recent feeding experiments indicate that the primary objective in feeding the lactating sows is to maximize food intake. To achieve this, gestation food intake must be held low, high environmental temperatures must be avoided, high density lactating sow diets should be fed, and the fat content of the sow at farrowing should be controlled (Hughes, 1989). Feeding ad libitum should be practised during lactation, at least to first and second litter sows (e.g. Håkansson et al., 1993). Feeding ad libitum should, however, not begin immediately after farrowing, but the amount of food should be gradually increased to free access during the first 2–3 days after farrowing. An immediate change to feeding ad libitum at farrowing resulted in a high incidence of agalactia post partum (Håkansson et al., 1993).

Metabolism During Late Gestation and Early Lactation

A well fed sow is in an anabolic state during mid-gestation, resulting in deposition of fat and protein in both maternal and fetal tissue (Close et al., 1985). Depending upon the energy and nutrient supply, the sow may mobilize body reserves during late gestation and become catabolic when the growth of the fetuses is greatest. This change to catabolic state is reflected by decreasing insulin concentrations (Simoes Nunes et al., 1987) and increasing serum concentrations of free fatty acids and urea nitrogen (Ruiz et al., 1971).

After parturition, suckling stimulates the release of prolactin and oxytocin. These hormones have been found to promote the utilization of maternal stores of energy and protein for milk synthesis. In rats, prolactin has been shown to induce an increase in the number of insulin receptors in the mammary gland and a decrease in their number in maternal fat (Flint et al., 1981; Flint, 1982). Oxytocin, however, mobilizes glucose from maternal stores and contributes to its deposition in the mammary gland (Altszuler and Hampshire, 1981; Stock and Uvnäs-Moberg, 1985). Suckling also influences the gut hormones gastrin and somatostatin in sows (Uvnäs-Moberg et al., 1984). The increase in gastrin and decrease in somatostatin that occurs in response to suckling probably leads to an increased digestive capacity.

The rate at which maternal fat depots are mobilized in sows during lactation, reflected by a loss of weight and a decrease in backfat thickness, is influenced by body weight and backfat thickness at farrowing (Yang et al., 1989; Rojkittikhun et al., 1992), litter size (Yang et al., 1989; Sterning et al., 1990), litter weight gain (Sternling et al., 1990) and lactation feeding (Johnston et al., 1986; Yang et al., 1989). The rate of maternal fat mobilization varies considerably among sows (Reese et al., 1984; Sterning et al., 1990) and the variation in weight loss is also large among sows fed the same amount of feed and nursing the same number of piglets (Sternling et al., 1990). This finding indicates that there may be individual differences in energy metabolism between equally nourished sows with the same performance during lactation (Rojkittikhun et al., 1992). A high estimate of heritability was also found for weight loss during first lactation (Rydhmer et al., 1992).

Energy metabolism during late gestation and lactation in relation to backfat thickness was studied in multiparous sows (Hultén et al., 1993). The sows were divided into two groups – high (H) and low (L) – according to their backfat thickness 9 days before parturition. The sows were fed the same diet (11.9 MJ kg⁻¹ body weight, 14.5% crude protein). During gestation feed intake was 2.2 kg day⁻¹, while during lactation it was 3.0 kg day⁻¹ plus 0.4 kg per piglet nursed. Sow weight loss was greatest during the first week of lactation. This loss was most evident in the H-group, amounting to 14.0 kg during the
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first week of lactation and a total of 16.6 kg during the first three weeks. Corresponding values for the L-group were 4.2 and 6.5 kg, respectively. The difference in weight loss between the two groups was significant during the first week \( (P < 0.05) \). Backfat thickness decreased in both groups 9 days before farrowing until 21 days of lactation, but the decrease was highest in the H-group \( (P < 0.05) \). The blood concentrations of glucose, urea nitrogen, creatinine, triglycerides, free fatty acids and \( \beta \)-hydroxy butyric acid are shown (Table 1). In both groups the concentrations of free fatty acids were low on day 9 before parturition, while those of triglycerides were high indicating anabolism. During the first week of lactation, the concentrations of free fatty acids increased in the H-group but not in the L-group and the concentrations of urea nitrogen were higher in the H-group. These differences, together with the greater loss of weight observed in the H-group, indicate that catabolism of maternal fat and protein depots was more pronounced in the H-group than in the L-group during this time. On day 14 of lactation, both groups showed equally low concentrations of free fatty acids, decreasing creatinine concentrations and stable triglyceride and urea nitrogen concentrations. Furthermore, weight loss during the second and third weeks of lactation was low in both groups. The results from this study indicate that under a restricted feeding regimen the catabolic rate during the first week of lactation is higher in sows with higher backfat thickness in late gestation. As lactation progresses, a more balanced metabolism is achieved regardless of backfat thickness before parturition.

After 5 weeks of lactation primiparous sows were divided into a low-weight-loss group (LWL-group, loss < 25 kg) and a high-weight-loss group (HWL-group, loss > 25 kg) (Rojkittikhun et al., 1993a). All sows were fed a diet containing 14.9% crude protein and 12.1 MJ kg\(^{-1}\) body weight digestible energy. The daily feed allowance was gradually increased from 2.2 kg at farrowing to a maximum of 3.0 kg plus 0.4 kg per piglet. The HWL-group sows lost weight throughout lactation, whereas the LWL-group sows gained weight during the last week. Weight loss was higher in the HWL-group than in the LWL-group during weeks 2, 3 and 5 of lactation. Catabolism of adipose tissue, indicated by a decrease in insulin and an increase in glucagon and non-esterified fatty acids (NEFA) and muscle proteins (indicated by high creatinine), was observed in both groups during the first week of lactation. This catabolic state was more pronounced and tended to be prolonged in the HWL-group. Concentrations of all metabolic parameters measured seemed to be stable in both groups during the last two weeks of lactation. Changes in body weight and in concentrations of metabolites in the blood indicate that the HWL sows need a longer period to compensate for their negative energy and protein balance during lactation. The results from a previous report (see above; Hultén et al., 1993) indicated that weight loss was greatest during the first week of lactation in multiparous sows, especially in sows with a thick backfat layer at farrowing. It is likely that high-weight-loss primiparous sows need a longer period to recover from their negative energy balance during lactation than do low-weight-loss primiparous sows or multiparous sows.

Feeding-related Endocrine Changes During Lactation

Feeding stimulates the release of prolactin and oxytocin in the sow (Uvnäs-Moberg et al., 1985; Armstrong et al., 1986). It was suggested that release of oxytocin induced by feeding may be the result of release of cholecystokinin (CCK) in the gut associated with food intake as i.p. injection of this peptide increases oxytocin concentrations in rats (Verbalis et al., 1986). The effect of fasting for 24 h and refeeding on the release of oxytocin, prolactin, insulin and CCK was investigated in lactating primiparous sows (Rojkittikhun et al., 1993c; Fig. 1). The sows were starved, but supplied with water ad libitum, from 09:00 h on day 27 of lactation until 15:00 h on day 28, when they were refeed. Blood samples were collected continuously, using an automatic collection system adapted for sow with piglets moving free around her in the pen (Rojkittikhun et al., 1991a). The number of nursings was not influenced by the fasting and the refeeding. Concentrations of insulin and glucose in plasma decreased to very low values during fasting and increased after refeeding. Plasma CCK increased significantly after refeeding. After fasting, concentrations of prolactin were low, and suckling did not induce significant release of prolactin. However, prolactin increased rapidly after refeeding. The mechanism underlying the relationship between the state of feeding and prolactin may be multifactorial. The rapid increase in prolactin following refeeding indicates that a neural mechanism may be involved. In earlier studies in rats, CCK has been shown to set up activity in afferent vagal fibre (Verbalis et al., 1986). The rise in CCK after refeeding
Table 1. Serum concentrations of energy and protein metabolites in pregnant and lactating sows with high or low backfat thickness (least square means)

| Energy and protein metabolites | Day after parturition | P-value, effect of Backfat thickness (H or L) | Day Backfat |
|-------------------------------|-----------------------|--------------------------------------------|-------------|
|                               | -9        | 2     | 7     | 14    | 21    |                          |                         |
| Glucose (nmol l⁻¹)            | 4.17ᵇ      | 4.71ᵇ | 5.45ᵇ | 5.33ᵇ | 5.42ᵇ | <0.001            | 0.92                |
| Urea (nmol l⁻¹)               | 3.55ᵇ      | 3.56ᵇ | 4.14ᵇ | 4.99ᵇ | 5.14ᵇ | <0.001            | 0.02                |
| Creatinine (µmol l⁻¹)         | 175ᵇ       | 165ᵇ  | 165ᵇ  | 143ᵇ  | 138ᵇ  | <0.001            | 0.39                |
| Triglycerides (µmol l⁻¹)      | 640ᵇ       | 332ᵇ  | 332ᵇ  | 275ᵇ  | 322ᵇ  | <0.001            | 0.83                |
| Free fatty acids (µmol l⁻¹)   | 261ᵇ       | 352ᵇ  | 277ᵇ  | 117ᵇ  | 87ᵇ   | <0.001            | 0.01                |
| β-Hydroxybutyric acid (µmol l⁻¹) | 389ᵇ   | 241ᵇ  | 246ᵇ  | 245ᵇ  | 243ᵇ  | <0.001            | 0.38                |

Values within rows followed by different letters differ significantly (P < 0.05).
Data reproduced with permission from Hultén et al. (1993).
Number of animals = 10.
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Fig. 1. Concentrations of oxytocin, prolactin, LH and insulin in one of the sows measured during a 6 h period after 24 h of fasting and after refeeding using a continuous collection technique. Oxytocin was analysed in all samples collected at 4 min intervals except during nursing when samples were collected every minute (samples were not pooled). Aliquots of plasma were combined to form pooled 8 min samples for the measurement of insulin, prolactin and LH concentrations. Glucose concentrations were measured from 4 min samples obtained every 30 min. Aliquots of plasma collected from 14:00 to 17:00 h were combined to form pooled 16 min samples for determination of cholecystokinin (CCK) concentrations. Periods of suckling are indicated by the black bars. The hatched bar indicates the duration of eating (refeeding started at 15:00 h). (Reproduced with permission from Rojkittikhun et al., 1993c).

therefore suggests that vagal nerve afferents were activated and subsequently pathways to the hypothalamus, and this may partly relate to the increase in prolactin (Rojkittikhun et al., 1993c). These data indicate that the effect of suckling, the major mechanism controlling release of prolactin and oxytocin during lactation, is reinforced by neural activity from the gastrointestinal tract.

Baidoo and Aheme (1988a, b) demonstrated that plasma concentrations of FSH before weaning, and those of FSH and LH after weaning, were significantly higher in sows fed ad libitum during lactation than in sows fed 50% of the ad libitum intake. A low level of feeding during lactation resulted in greater weight and backfat loss, higher plasma concentrations of GH and cortisol, and lower concentrations of insulin during lactation. Kirkwood et al. (1987) and Plaine et al. (1992) found lower basal LH concentrations during lactation in poorly fed sows (3 kg and 2.2 kg daily, respectively) than in sows fed ad libitum. Tokach et al. (1992) characterized LH secretion during lactation in primiparous sows that experienced an early (<9 days) or late (>15 days) return to oestrus after weaning. Sows had a higher mean LH that returned to oestrus early and more LH peaks per 6 h on days 14, 21 and 28 and higher serum insulin on days 7 and 21 than did late sows (Tokach et al., 1992). They also found that insulin concentration on day 7 was correlated with the number of LH peaks on day 14 (r = 0.50), day 21 (r = 0.70) and day 28 (r = 0.43).

Tokach et al. (1992) concluded that alterations in LH profile as early as day 14 of lactation are associated with a delayed return to oestrus after weaning, and that insulin concentrations during early lactation may be associated with subsequent reproductive function.

The release of GnRH by the hypothalamus is suppressed during lactation, thereby inhibiting the synthesis and release of LH. Ovulatory oestrus can, however, be successfully induced in some lactating sows through pulsatile injections of GnRH (e.g. Rojanasthien et al., 1988). A 24 h fast (days 27–28) in lactating sows decreased prolactin to post-weaning values, whereas LH secretion, oxytocin release and suckling frequency were the same as after refeeding (Rojkittikhun et al., 1993c). These findings indicate that short-term starvation, resulting in low plasma concentrations of prolactin and of insulin and glucose, does not influence LH release in lactating sows. At certain doses, intracerebroventricular administration of insulin increased peripheral concentrations of LH and LH pulse frequencies in ovariectomized gilts.
indicating that insulin may stimulate LH release (Cox et al., 1989). However, no significant relationship was seen between LH and insulin on either day 10 or day 20 of lactation by Rojkittikhun et al. (1993b). LH secretion was also similar between the periods of low and high plasma insulin during short-term starvation and refeeding, respectively (Rojkittikhun et al., 1993c). These findings indicate that the changes in plasma concentrations of endogenous insulin do not influence LH release in lactating sows. However, a prolonged decrease in insulin concentrations due to long-term starvation may affect LH secretion in lactating sows. Further studies are necessary to elucidate the somewhat different results of Tokach et al. (1992) and Rojkittikhun et al. (1993b, c).

**Body Weight Loss Associated with Lactation, Metabolic and Reproductive Hormones and Interval from Weaning to Oestrus**

Several investigations have demonstrated that sows losing excessive amounts of body weight will have extended weaning to oestrous intervals and an increase of anoestrus (e.g. King et al., 1982, 1984; Reese et al., 1982a, b; King and Williams, 1984a, b). The level of weight or condition loss below which an extension in the remating interval will occur and the level of dietary energy intake required to prevent this is unknown (Aherne and Kirkwood, 1985).

Weaning is normally related to an increase in LH concentration in terms of basal values and LH pulses, even if stimulation of follicular development is not necessarily associated with a measurable change in circulating gonadotrophins (Cox and Britt, 1982; Shaw and Foxcroft, 1985; Foxcroft et al., 1987). Several workers have suggested that mean LH concentrations and pulse frequency of LH secretion decreased in sows underfed during lactation (Kirkwood et al., 1987; Mullan and Close, 1989). Armstrong et al. (1986) found that the weaning to remating interval was shortest in the sows with the highest LH pulse frequency before weaning. Their results, from an experiment in which primiparous sows were fed either ad libitum or feed restricted during lactation, demonstrated that diet had no effect on plasma LH or subsequent reproductive performance. In addition, weight and backfat changes during lactation were identical between oestrous and anoestrous sows. Backfat changes during lactation, however, were related to the weaning to oestrous interval in those sows that showed oestrus within 8 days after weaning. Similar results were reported by Sterning et al. (1990), demonstrating a significant positive correlation between weight loss and interval from weaning to first standing oestrus among primiparous sows, showing ovulatory oestrus within 10 days of weaning.

The plasma concentration of cortisol shows a diurnal rhythm in pigs. No diurnal rhythm, however, was observed on the day of weaning and cortisol remained high (Rojkittikhun et al., 1991b), indicating that short term stress is induced by weaning. Weaning also results in decreases in plasma glucagon and gastrin, but increases in insulin and somatostatin (Rojkittikhun et al., 1991c). Plasma glucose remained unchanged after weaning, which might indicate that insulin concentrations were increased and glucagon concentrations decreased to lower glucose concentrations. After weaning, nutrients that are meant to be incorporated into milk, such as glucose, might accumulate in the circulation until the maternal metabolism has returned to its nonlactating state. The changes in gastrin and somatostatin secretion after weaning might reflect the loss of the suckling-related influence of gastrin and somatostatin secretion together with a decrease in the local trophic effect of feeding after weaning, since the amounts of feed provided for each sow were slowly reduced to the non-lactating level (Rojkittikhun et al., 1991b).

In a further study of endocrine and metabolic changes associated with weaning, conventionally fed primiparous sows with a similar number of piglets were assigned to three groups according to their body weight loss after a 5-week lactation period as follows: H-group (loss > 25 kg), M-group (loss 11–25 kg) and L-group (loss < 10 kg). Sows, with low body-weight loss during lactation, had higher plasma insulin and lower plasma cortisol than sows with high weight loss (Rojkittikhun et al., 1992). The differences between groups of sows were more pronounced during the period after weaning. No differences in plasma glucagon and glucose were found. Despite the different metabolic status at weaning, no significant differences in the duration of the interval from weaning to oestrus or in plasma LH and oestradiol were observed in this study. This indicates that the losses of body reserves in these sows were not beyond their physiological capacity to resume normal cyclicity. The similarities found in the interval
from weaning to oestrus and concentrations of LH and oestradiol at weaning among all groups of sows in this study are in accordance with the findings of Armstrong et al. (1986). However, differences in reproductive performance and reproductive hormone concentrations among sows differing in their degree of body weight loss may have been demonstrated if more animals had been included in this study (Rojkittikhun et al., 1992). The mechanism by which metabolic status at weaning influences reproductive function in sows needs further study.

**Conclusion**

The metabolic state of lactating sows, reflecting the balance between nutrient intake and milk production in lactation, should potentially regulate differences in reproductive performance after weaning. The absence of such effects either relates to our failure to refine experimental techniques to measure appropriate indices of metabolic and reproductive activity adequately, or may be due to high inherent fertility in sows under present systems of management.

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