Impact of Postovulatory Food Deprivation on the Ova Transport, Hormonal Profiles and Metabolic Changes in Sows

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Razdan P, Mwanza AM, Kindahl H, Hultén F, Einarsson S: Impact of post-ovulatory food deprivation on the ova transport, hormonal profiles and metabolic changes in sows. Acta vet. scand. 2001, 42, 45-55. – The effect of food deprivation on ova transport, hormonal profiles and metabolic changes was studied in 20 crossbred multiparous sows during their second oestrus after weaning. To determine the time of ovulation, transrectal ultrasonographic examination was performed. The sows were divided into 2 groups, one control group (C-group), which was fed according to Swedish standards, and one experimental group (E-group). The E-group sows were deprived of food from the first morning meal after ovulation until slaughter. Blood samples were collected every second hour from about 12 h before expected ovulation in the second oestrus after weaning until slaughter and were analysed for progesterone, prostaglandin $F_{2\alpha}$-metabolite, insulin, glucose, free fatty acids and triglycerides. All sows were slaughtered approximately 48 h after ovulation and the genital tract was recovered. The isthmic part of the oviduct was divided into 3 equally long segments and flushed separately with phosphate buffered saline (PBS). Uterine horns were also flushed with PBS. A significantly greater number of ova were found in the first and second part of the isthmus in the E-group ($p = 0.05$) while in the C-group most of the ova were found in the third part of the isthmus or the uterus ($p = 0.01$). The level of prostaglandin $F_{2\alpha}$-metabolite was significantly higher in the E-group compared with the C-group. The concentration of progesterone increased in both groups after ovulation but there were no significant differences between the groups. The other blood parameters showed that the food-deprived sows were in a catabolic state. The 48 h period of fasting results, directly or indirectly in an delayed ova transport, which may be due to a delayed relaxation in the smooth circular muscle layer of the isthmus.

sow; isthmus; ova transport; prostaglandin F_{2a}; progesterone; metabolism; stress; reproduction; nutrition.

Introduction

Due to welfare considerations, as well as the urge for a more efficient production, group housing of sows has been an overall common management practice in modern pig production. Mixing of the sows in these regimes is in general done after mating and, when a new rank order is established among sows aggressive interactions are common (*Mendel et al.* 1992, *Tsuma et al.* 1996b). It is not unusual for the more submissive animals to have less or no access to food (*Brouns et al.* 1994). This means that the sows are exposed to stress in perhaps the most sensitive stage of gestation since it has been shown that most embryo mortality occurs

before day 10 of pregnancy (*Lambert et al.* 1991). Stress is associated with hormonal and metabolic changes and has a negative effect on reproductive performance (*Mburu et al.* 1998, *Mwanza et al.* 2000a, *Tsuma et al.* 1996b) but the exact mechanisms mediating these effects are not fully understood. A statistically significant rise in blood plasma concentration of cortisol after 2 days of food deprivation has already been shown in the studies of *Mburu et al.* (1998) and *Tsuma et al.* (1996a).

Progesterone as a potential mediator of the nutritional status during early pregnancy and its influence on embryo survival, oviductal and endometrial development has been thoroughly investigated and widely discussed (*Ashworth et al.* 1991, *Buhi et al.* 1990, *Jindal et al.* 1996, *Jindal et al.* 1997, *Mao et al.* 1998, *Mburu et al.* 1998, *Pharazyn et al.* 1991, *van der Lende et al.* 1994). It is generally agreed that an abnormal change in the blood plasma progesterone levels after ovulation might induce a slight asynchrony between embryonic and uterine development which in turn might reduce embryo viability (*Pope* 1988). *Mburu et al.* (1998) found that food deprivation immediately after ovulation hastened the physiological increase in blood plasma progesterone and retarded cleavage rate of the ova as well as decreased the number of spermatozoa in the oviductal reservoir.

The objective of the present study was to investigate if there is any correlation between the changes in the hormonal profiles and the ova transport time after stress caused by food deprivation and if the earlier argued asynchrony between the gamete and uterine development may partly be explained by a change in the transport time of the ova.

Materials and methods
Animals
The experiment was performed with a total of 21 crossbred (Swedish Landrace × Swedish Yorkshire) sows in their second to fourth parity. The weight of the sows was between 155-240 kg when they were brought from a commercial farm on the day of weaning. They were placed in individual pens on straw at the Department of Obstetrics and Gynaecology, Swedish University of Agricultural Sciences, Uppsala, Sweden. The sows were studied during 2 oestruses where the first oestrus after weaning was used to predict the interval from onset of standing heat to ovulation in the second oestrus of each sow (*Mburu et al.* 1995). The sows were fed 2.9 kg of a commercial ration divided into 2 meals at 7:00 am and 3:00 pm, according to Swedish standards (*Simonsson* 1994). Water was provided *ad libitum.* The sows were randomly divided into 2 groups, one control group (C, n =10), which continued to be fed as above and one experimental group (E, n =11) deprived of four meals of feed starting with the first morning meal after the second ovulation. One of the E-group sows was excluded from the experiment due to injury and had to be slaughtered 18 h after ovulation. Two of the remaining 20 sows, one from each group, had to be excluded from the blood sampling part of the study due to failing jugular vein catheters.

Oestrous detection and ovulation
Detection of oestrus was performed twice a day (morning and evening) from mid pro-oestrus and every 4 h from late pro-oestrus by testing the sows with back-pressure in front of a boar. Standing oestrus was defined as when the sows were standing to back pressure in the presence of a boar. The time of ovulation was determined through transrectal ultrasonography. An annular array sector scanner (type Scanner 250, Pie Medical b.v Maastricht, the Netherlands) with a 5 MHz multiple scan angle transducer was used as described by *Mburu et al.* (1995). Ultrasonography was performed every fourth hour

from about 20 h after the onset of oestrus and until ovulation had occurred. The time of ovulation was set as the time when all large follicles had collapsed.

Blood sampling

A few days before the second oestrus after weaning was expected (days 15-18), a permanent silastic tubing was inserted into the right jugular vein (*Rodriguez-Martinez et al.* 1983). The silastic tubing was passed subcutaneously to the back and exteriorized through the skin where it was connected to a cannula to make blood collection easy and free from stress for the sows. The tubings were flushed twice daily with heparinized saline (25 IE/ml) until the blood collection began.

Blood collection in heparinized tubes started 12 h before expected ovulation in the second oestrus after weaning and was performed every second hour until the sows were slaughtered. The heparinized tubes were immediately centrifuged at a speed of 3000 rpm for 10 min and the collected plasma was frozen and stored at –20 °C. At 10 am and 6 pm blood was also collected in tubes without additive. Before storage, and in a period of 30 to 60 min after sampling, the tubes were centrifuged twice at the same speed and duration as above.

Slaughter and recovery of the ova

The sows were slaughtered at approximately 48 h after ovulation and the genital tract was immediately recovered. After the corpora lutea had been counted in each ovary, the uterine horns on both sides were separated from the uterine body and flushed separately with 100 ml of 37 °C warm phosphate buffered saline (PBS). The length of the isthmus was estimated by the thickness of the oviductal wall, after which, the isthmic part of the oviduct was divided into 3 equally long segments. The isthmic segments were flushed separately with 40 ml of

PBS. Most of the flushing fluid was filtered away before the remaining volume was examined under a light microscope and the ova present in each part were counted.

Hormone assays

Prostaglandin metabolite. The main initial blood plasma metabolite of prostaglandin $F_{2\alpha}$, 15-keto-13,14-dihydro-$PGF_{2\alpha}$ (15-ketodihydro-$PGF_{2\alpha}$), was analysed by radioimmunoassay as described previously by *Kunavongkrit et al.* (1983). The relative cross-reactions of the antibody were 16% with 15-keto-$PGF_{2\alpha}$, 4% with 13,14-dihydro-$PGF_{2\alpha}$ and 0.4% with $PGF_{2\alpha}$. The intra-assay coefficients of variation ranged between 3.4% and 7.6% for different ranges of the standard curve and the inter-assay coefficient of variation was approximately 14%.The practical limit of sensitivity for the assay, analysing 0.2 ml of plasma, was 60 pmol/l.

Progesterone. The concentration of progesterone (P_4) in peripheral blood plasma was determined using an enzyme immunoassay (Amerlite, Kodak Clinical Diagnostics Ltd., Amersham, England). The kit was used according to the manufacturer's instructions with the following modifications: to increase the sensitivity of the P_4 assay, both the assay reagent (rabbit anti-progesterone) and the conjugate reagent (HPR-labelled progesterone) were diluted 1:2 with saline solution. To produce a new standard curve, standard B (plasma containing 2 nmol/l of P_4) was diluted with standard A (human 0-plasma) to 1.0, 0.5 and 0.25 nmol/l, which resulted in a standard curve with following concentrations: 0, 0.25, 0.5, 1.0, 2.0 (standard B) and 8.0 (standard C). Serial dilutions of porcine plasma produced displacement curves parallel to the standard curve. The intra-assay coefficients of variation calculated from 10 assays were below 10% for concentrations between 0.25 and 8 nmol/l. The inter-assay co-

efficient of variation for one control sample was 11% (2 nmol/l). The average detection limit of the assay was 0.2 nmol/l.

Insulin. Plasma samples were analysed by radioimmunoassay for insulin determination (Insulin RIA 100, Pharmacia Diagnostics AB, Uppsala, Sweden) (*Mburu et al.* 1998). Serial dilutions of porcine plasma with high insulin concentrations produced inhibition curves parallel to the standard curve. Intra-assay coefficients of variation were 7.4% (0.93 μU/ml), 4.9% (2.01 μU/ml) and 5.8% (5.80 μU/ml), for low, medium and high assay controls, respectively. The average detection limit of the assay was 1 μU/ml.

Blood serum metabolite assays

Triglycerides. Blood serum triglycerides were analysed with an enzymatic colorimetric method (GP/PAP method) with a Cobas MIRA analyzer (Roche, Basel, Switzerland) using reagents from the same company (UNIMATE 5 TRIG). The intra-assay coefficient of variation was 1.2% (1.4 mmol/l) and the inter-assay coefficient of variation was 4% (1.4 mmol/l).

Free fatty acids. Blood serum free fatty acids were analysed on Cobas FARA (Roche) with reagents from W (NEFA C, Wako chemichals GmbH, Neuss, Germany). The intra-assay coefficients of variation for 2 quality control samples were 3% (0.4 mmol/l) and 2% (0.8 mmol/l) and the corresponding inter-assay coefficients were 5.7% and 6.4%, respectively.

Glucose. Serum levels of glucose were determined on Cobas MIRA (Roche with an enzymatic method (HK/G6P-DH method). Standardised reagent kits (Unimate 5 Gluk HK, Roche) were used. The intra-assay coefficient of variation was 1.3% (7.5 mmol/l) and the inter-assay coefficient was 3.5% (5.5 mmol/l).

Statistical analysis

The statistical analyses were carried out using SAS- procedures (*SAS Institute Inc.* 1989). The t-test in the MEANS procedure was used to make comparisons between the groups of mean values for the ovulation rate, ova recovery rate, time elapsed from the time of ovulation to onset of fasting and time of slaughter. Fisher´s Exact test (2-tail) was used to compare the number of ova recovered in the upper part of the isthmus (segments 1 and 2) with the number of ova found in the lower part of the genital tract (segment 3 and uterine horn) within each group. To make between-group comparisons with regard to degree of transit of ova at the time of slaughter, the total number of ova detected in each segment (the sum total of both sides of the oviducts in each sow) was multiplied with Factor 1-4, depending on which of the 4 segments contained the ova (proximal isthmus=1, middle isthmus=2, distal isthmus=3, uterus=4) (*Hultén et al.* 2000). The sum was divided by the total number of ova recovered for each sow giving average number of segments the ova had covered at the time of slaughter within each sow. The data was analysed by the GLM procedure and the model included treatment and interval, from ovulation to slaughter. In the 2 groups, overall mean values for the period before and after start of treatment respectively, were calculated for glucose, insulin, free fatty acids and triglycerides and between group comparison was performed using the t-test. Plasma was collected on 6 occasions for progesterone and prostaglandin $F_{2\alpha}$-metabolite analyses during five 12 hour periods, one period before and 4 periods after time 0. For progesterone, time 0 was set as the time of ovulation because of the physiological rise in P_4, which is expected after ovulation, whereas for prostaglandin $F_{2\alpha}$-metabolite time 0 was the start of food deprivation. The observations at time 0 were included in the first period (-11 to 0 h). Mean values were calculated for each 12 hour period and these values were analyzed by the GLM-procedure in

Table 1. Interval from ovulation to first morning meal (f.m.m) after ovulation = start of treatment, and from ovulation to slaughter, ovulation rate (no. of corpora lutea) and recovery rate (no. of ova found / no.of corpora lutea) (Mean ± SEM).

	C-group	E-group	p-value
Interval from ovulation to f.m.m (h)	10.5 ± 2.1	10.5 ± 1.9	1.0
Interval from ovulation to slaughter (h)	42.3 ± 1.9	45.0 ± 1.6	0.3
Ovulation rate	14.6 ± 1.1	15.6 ± 1.1	0.5
Recovery rate (%)	77.7 ± 6.4	78.9 ± 3.8	0.9

the SAS package (*SAS Institute Inc.* 1989). The statistical model included the effect of group, sows within group, 12 h period and the interaction between group and period. Sow within group was used as error of term.

Results

Recovery and distribution of ova

There was no significant difference between the 2 groups in ovulation rate, ova recovery rate, time elapsed from ovulation to start of treatment/first morning meal or ovulation to slaughter (Table 1). The distribution of ova in the isthmus and the uterine horn differed significantly between the 2 groups (Table 2). The E-group sows had a significantly (p = 0.05) higher frequency of ova in the proximal and middle isthmus compared to the C-group, while C-group sows had a significantly (p = 0.01) higher frequency of ova in the distal part of the isthmus and in the uterus. The ova in the E-group had on average passed 1.4 segments at time of slaughter while in the C-group ova had passed 3.0 segments on average which was significantly (p = 0.001) longer.

Hormones and blood serum metabolites

There was no difference in the pre-fasting (-14 to 0 h) plasma level of insulin between the C-group (11.5 ± 2.7 μU/ml) and the E-group (11.3 ± 1.8 μU/ml) (Fig. 1). The plasma level of insulin for the E-group sows decreased during the fasting period to an average of 6.4 ± 0.6 μU/ml which was significantly different from the C-group levels of 13.1 ± 3.5 μU/ml (P <0.001) during the same period. The serum levels of free fatty acids were significantly (p = 0.01) higher in the E-group (0.49 ± 0.09) compared with the C-group (0.16 ± 0.04) after start of food deprivation (Fig. 2). There were no significant changes in the glucose and triglyceride levels before or after the start of food deprivation and there were no significant differences between the groups (Figs. 3 and 4 respectively). Progesterone. The plasma P_4 concentration in both the E-group and C-group increased af-

Table 2. The distribution of the total number and percent of ova in the isthmus and uterine horns at the time of slaughter.

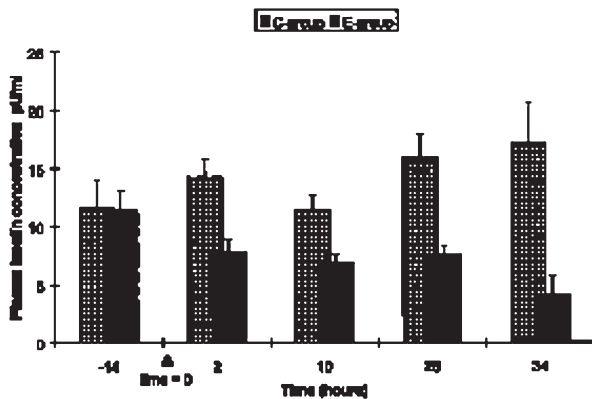|	Proximal No. (%) of ova	Isthmus-middle	distal	Uterine-horn	Total
E-group	35 (40)	36 (41.5)	16 (18.5)	0 (0)	87 (100)
C-group	4 (4)	18 (18)	47 (47)	31 (31)	100 (100)

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Figure 1. Plasma insulin (means ± SEM) before and after time 0 = start of treatment.
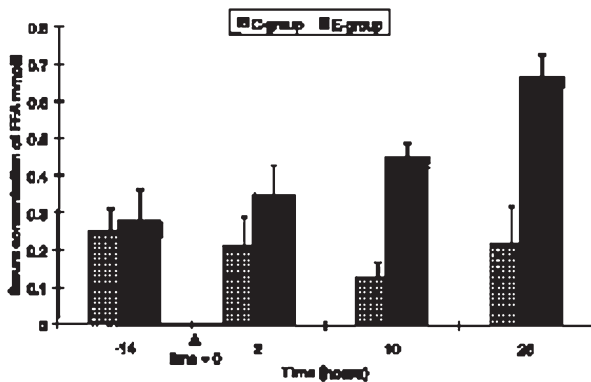

Figure 2. Serum levels of free fatty acids (means ± SEM) before and after time 0 = start of treatment.
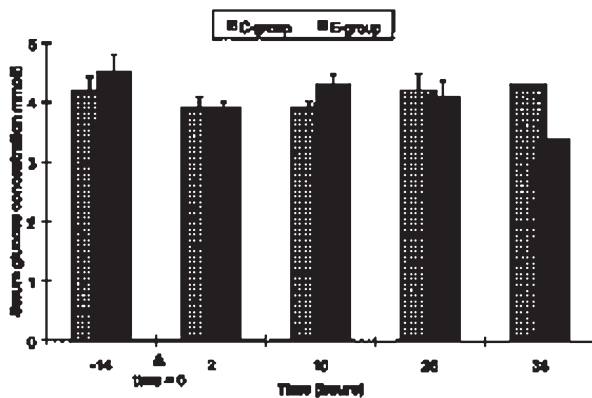

Figure 3. Serum levels of glucose (means ± SEM) before and after time 0 = start of treatment.
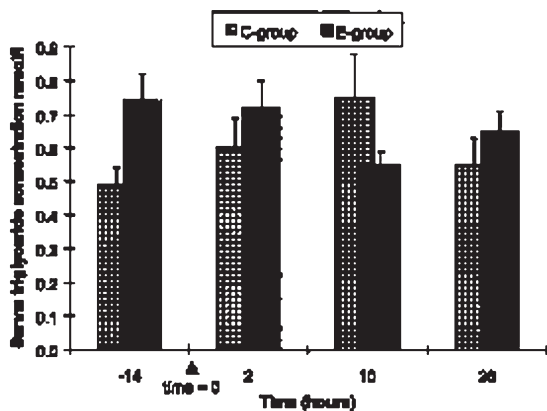
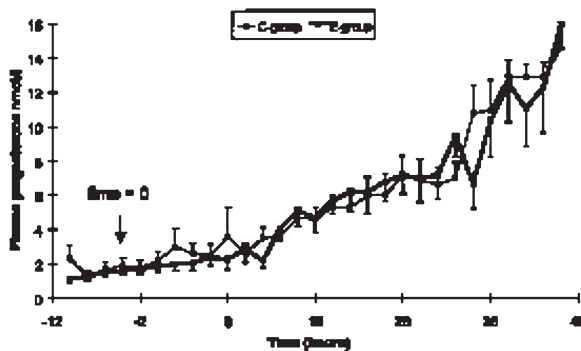Figure 4. Serum levels of triglycerides (means ± SEM) before and after time 0 = start of treatment.

Figure 5. Plasma levels of progesterone (means ± SEM) before and after time 0 = time of ovulation.
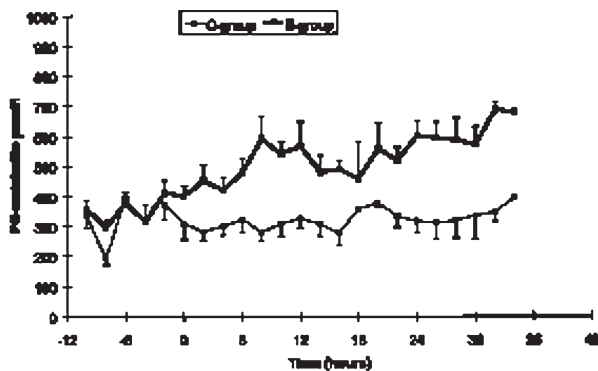

Figure 6. Levels of prostaglandin $F_{2\alpha}$-metabolite (means ± SEM) before and after time 0 = start of treatment.

ter ovulation (Fig. 5). Both groups had a significantly (p = 0.001) higher concentration of P4 in the period, 13 to 24 h after ovulation, compared with the period -11 h to 0 h (0 = time of ovulation) and it continued to increase. There were no significant differences between the 2 groups before or after the ovulation.

Prostaglandin metabolite. The plasma levels of the prostaglandin metabolite (15-ketodihydro-PGF$_{2\alpha}$) were significantly (p = 0.0001) higher in the E-group compared with the C-group during the fasting period, while there were no significant differences between the groups in the prefasting period (Fig. 6).

Discussion

It has been suggested that the development of embryos during oviductal transit is affected by the rate at which they are transported to the uterus (*Hunter* 1988). The food deprived sows had a significantly greater number of ova in the proximal and middle part of the isthmus compared to the control sows, whereas the control sows had most of their ova in the distal part of the isthmus and uterine horns. This indicates that fasting, either directly by inducing a change in the metabolism, or indirectly via the effect of stress and the hormonal changes induced by stress, lowers the rate at which the ova are transported through the oviduct. The circular muscle layers of the isthmus are very richly innervated, with high densities of adrenergic nerve terminals (*Hunter* 1988, *Rodriguez-Martinez et al.* 1982). The dense adrenergic innervation permits the isthmus to act as a physiological sphincter which may be important for regulating the transport of gametes. It has also been shown in in vitro studies of the oviduct that the isthmus during the period of ova retention in the ampulla-isthmic junction, reacts more strongly to noradrenaline and adrenaline suggesting the existence of an adrenergic sphincter (*Rodriguez-Martinez* 1984).

Mwanza et al. (2000b) found a deviant isthmic motility pattern in fasted sows. In control sows there was a decrease in the luminal isthmic pressure after ovulation; this decrease was delayed in the fasted sows and they also had higher frequencies of phasic pressure fluctuations in the isthmus during the same period. A delay in the opening of the ampullary isthmic junction could have restricted ova displacement through the isthmus (*Mwanza et al.* 2000b). One explanation could be that stress in general causes an up-regulation of the sympathetic nerve-system, which induces contraction of the smooth muscles, creating a physiological sphincter in the oviduct.

The fasted sows had a significantly higher blood plasma concentration of the PGF$_{2\alpha}$-metabolite than the control sows from 6 h after ovulation and onwards (Fig. 6). Prostaglandin F$_{2\alpha}$ has been shown to increase the in vitro motor activity of the isthmus and its circular muscle layer, especially during day 3 of the oestrous cycle (*Rodriguez-Martinez et al.* 1985). *Pettersson et al.* (1993) found that treatment with PGF$_{2\alpha}$ increased the frequency of phasic pressure fluctuations in a dose-dependent manner, supporting the theory that PGF$_{2\alpha}$ is involved in maintaining intraluminal pressure in the isthmus during proestrus. Before ovulation, there is a physiological decrease in the concentration of prostaglandin F$_{2\alpha}$-metabolite, which is associated with a decrease in isthmic pressure (*Mwanza et al.* 2000b). Therefore it may be speculated that an increase in the PGF$_{2\alpha}$-production, as reflected by the increased blood plasma concentration of prostaglandin F$_{2\alpha}$-metabolite, will further enhance the effect of the previously assumed stress-induced adrenergic response.

No significant difference was observed in P$_4$ levels between the groups (Fig. 5). This is not consistent with earlier findings where increased P$_4$ levels have been noted in sows deprived of

food at days 10-11 of pregnancy (*Tsuma et al.* 1996a) and direct after ovulation (*Mburu et al.* 1998). One reason for this may be that the effect of fasting on the plasma P_4 level occurs later than 36 h after the onset of food deprivation, meaning that such a change could not have been detected in the present study.

It may be that in our study the period of food deprivation was not long enough to substantiate any differences between the groups with respect to blood serum levels of glucose and triglycerides. Since stress induced glucocorticoid secretion stimulates glycogenesis and lipolysis, the food deprived animals would initially compensate for the lack of energy intake (*Varley et al.* 1994). This is confirmed by the significantly higher level of free fatty acids seen in the fasted sows while the low energy intake resulted in a significantly lower level of insulin during the fasting period. These endocrine changes indicate that the fasted sows were in a catabolic state, which is in agreement with the findings of *Mburu et al.* (1998) and *Mwanza et al.* (2000a). Insulin is thought to be one of the mediators of energy metabolism status and the reproductive development in prepubertal gilts (*Booth et al.* 1996). Further investigation is required in order to establish the importance of insulin as a mediator of nutritional effects and reproductive performance in sows.

The decrease in the transport rate of the ova could also be due to a change in the composition of oviductal fluid. The oviductal fluid is formed by selective transudation from the blood and active secretion from the endosalpinx (*Hunter* 1988). Accumulation of fluid in the oviductal lumen is programmed by the concentration of oestrogens and P_4 and there is evidence, to suggest that porcine oviductal tissue synthesizes specific oestrous-associated proteins at the time of fertilisation (*Buhi et al.* 1990, *Murray* 1993). It may therefore be speculated that a non-physiological hormonal change detected in

the peripheral circulation could also affect the composition of the oviductal fluid as well as the oviductal transport of the ova.

Conclusions

It can be concluded that stress induced by food deprivation immediately after ovulation decreased the concentration of insulin and increased the levels of free fatty acids and $PGF_{2\alpha}$ metabolite but had no effect on the levels of glucose, triglycerides or P4. Stress due to fasting also delayed ova transport through the isthmic part of the oviduct, which is probably an effect of many causes. One of these could be a prolonged α-adrenergic response (contractions) in the smooth circular muscle layers around the isthmus, although the exact mechanism of this phenomenon has to be further evaluated.

Acknowledgements

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Varley M, Stedman R: Stress and reproduction. In: Cole DA, Wiseman J, Valey MA (eds.). Principle of pig science. Nottingham University Press, Nottingham, U.K. 1994; pp 277-276.

Sammanfattning

Effekten av fasta direkt efter ovulationen på äggens transporthastighet genom äggledaren, hormonprofiler och metaboliska förändringar hos suggor.

Effekten av fasta direkt efter ovulering studerades på 21 korsningssuggor under deras andra brunst efter avvänjning. Suggorna delades in i 2 grupper, en kontrollgrupp och en försöksgrupp. För att fastställa ovulationstidpunkten gjordes rektal ultraljudsundersökning var fjärde timme från visad ståbrunst fram tills dess att inga folliklar kunde ses. Suggorna i försöksgruppen fastades från första morgonmålet efter ovulationen och fram till slakt medan kontrolldjuren utfodrades i enlighet med svensk norm. Blodprov togs varannan timme och användes för analys av progesteron, prostaglandin $F_{2\alpha}$-metabolit, insulin, glukos, fria fettsyror och triglycerider. Alla suggorna slaktades ungefär 48 timmar efter ovulering då livmodern togs ut tillsammans med äggledare och äggstockar för vidare undersökning. Istmus delades i tre lika långa delar, dessa spolades sedan med fosfatbuffertlösning (PBS). De nedre delarna av livmoderhornen spolades också med PBS. Signifikant (p = 0.05) fler ägg hittades i den första och andra delen av istmus hos försökssuggorna medan suggorna i kontrollgruppen hade de flesta äggen i den tredje delen av istmus och i livmodern (p = 0.01). Försöksgruppen hade signifikant högre nivåer av prostaglandin $F_{2\alpha}$-metaboliten än kontrollgruppen. Koncentrationen av progesteron steg i båda grupperna efter ovulationen, men det var ingen signifikant skillnad mellan grupperna. Blodparametrarna visade även att försökssuggorna, men inte kontrollsuggorna, hade en katabol metabolism under försöksperioden. Fasta under 48 timmar resulterade således i en fördröjd transport av äggen genom äggledaren vilket kan bero på en fördröjd minskning av kontraktionen hos de cirkulära lagren av glatt muskulatur i istmus.