Neth. J. agric. Sci. 28 (1980) 211-227

Relation between nutrition and fertility in pigs

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Accepted: 6 August 1980

Key words: energy intake, age at puberty, ovulation rate, conception rate, embryonic survival, fertility, gilt

Summary

Data from trials on the influence of intake of energy and protein on fertility in gilts were collected. According to calculations from several of the trials a high energy intake shortly before oestrus (flushing) increased ovulation rate. A low energy intake during rearing resulted in a fewer number of ovulations than a high energy level. But most or all of the favourable effect decreased because of a higher embryonic mortality. The sequence low, high, low for energy level during rearing, flushing and early pregnancy, respectively, seemed best. However, 3 out of 8 possible combinations have been widely studied.

Introduction

Before trials were started, we searched the literature on the relation between nutrition and fertility in pigs. The following characteristics were examined: age and weight at puberty; number of ovulations; conception rate; and embryonic survival.

Much research work has been undertaken on the relationship between nutrition and fertility in pigs. It is rather difficult to compare the different studies in this field because conditions in trials are so different: for example the age of the pigs and the kind of quantity (e.g. gross or net energy) or units (e.g. kcal or MJ) in which the requirements of the pigs are expressed are not the same. Another problem is that most trials are rather small and variation may be wide. Especially for studies on fertility, there is a need for large-scale experiments. Mostly nutrition or level of feeding is only a part of a wider aim. Joosten (1979) reviewed literature about the relationship between energy and fertility in pigs. He processed the data from literature to make it as comparable as possible. He used only exact data and expressed all the feeding levels as net energy rate for fattening (NE_F) (MJ/d) as is usual for pig nutrition in the Netherlands. The factors he used were: digestible energy (DE) = 0.8 × gross energy (GE); metabolizable energy (ME) = 0.96 × DE; $NE_F = 0.70 \times ME$.

In our study, we used statistical methods to combine the results of different studies on the influence of energy intake on reproduction in pigs and summarized a larger literature review of den Hartog (1980).

Material and methods

Data used for statistical processing were taken from 48 studies. The following characteristics were studied: embryonic survival, ovulation rate, age and weight at puberty and conception rate. The periods under study were: rearing, shortly before oestrus (flushing) and early pregnancy. Not all the possible combinations of treatments were covered in each study. We always compared treatments for each publication, since the factor publication brings together many variables like breed, season, housing and management.

In the statistical study, the following associations of food intake and reproduction traits were screened:

- energy intake during rearing with age and weight at puberty
- energy intake during rearing with ovulation rate
- energy intake shortly before oestrus with ovulation rate
- feeding level during rearing with conception rate
- energy intake during different periods with embryonic survival.

The periods were rearing, shortly before oestrus and early pregnancy.

The results of the different studies on the relation between food intake and fertility characteristics were combined by analysis of variance or covariance.

Results and discussion

Age and weight at puberty

Energy restriction

A gilt should reach puberty in a good condition and at an early age. Each day of delay in the first litter corresponded to a decrease of 0.02 to 0.03 piglets per sow per year (Legault & Dagorn, 1973). Before an age of 9 months, 60-90 % of gilts showed oestrus (Christenson & Ford, 1979). Swedish Landrace gilts reached puberty significantly earlier than Hampshire, Large White and Duroc gilts ($p < 0.01$). The heritability (h^2) of age and weight at puberty was 0.46 and 0.44 respectively (Legault, 1973). There are still other major factors influencing age and weight at puberty. Factors which reduce age at puberty according to Hughes & Cole (1975) are:

1. moving gilts to another pen (at a weight of about 55 kg)
2. daily contact with a boar (from a weight of about 64 kg)
3. genetic factors
4. ad libitum feeding during rearing.

Moving gilts to another pen and daily contact with a boar accelerate puberty (du Mesnil du Buisson & Signoret, 1962; Te Brake, 1975; Thompson & Savage, 1978). There is disagreement on the effect of nutrition on age and weight at puberty (Anderson & Melampy, 1972; Brooks & Cole, 1974; Rerat & Duée, 1975). Table 1

Table 1. Influence of energy or food restriction during rearing on age at puberty. There was calculated whether age at puberty was significantly increased or decreased by food restriction. If the effect was not significant, trials with 5 or more days difference were added to the trials with a significant effect. A decrease in age at puberty was taken as favourable and an increase as unfavourable.

Authors who found a favourable effect	Authors who found no effect	Authors who found an unfavourable effect
Self et al. (1955)**	Christian & Nofziger (1952)	Robertson et al. (1951)
Gosset & Sørensen (1959)	Lodge & McPherson (1961)	Burger (1952)
Hafez (1960)	Sørensen et al. (1961)	Haines et al. (1959)**
Aherne et al. (1976)	Holness (1972)	Zimmerman et al. (1960b)*
McPherson et al. (1977)**	Pay & Davies (1973)	Goode et al. (1965)*
	Etienne & Legault (1974)	O'Bannon et al. (1966)**
	Friend (1977)	Holness (1972)*
	Schilling & Schröder (1977)	Etienne & Duée (1973)**
		Duée & Etienne (1974)**
		Friend (1976)**
		van de Kerk & Elsinghorst (1976)*
		van Kempen (1976)*
		Schilling & Schröder (1977)
		Hermann & Richter (1979)

Significant difference: * $P < 0.05$; ** $P < 0.01$.

shows this inconsistency.

For statistical processing data of the following authors gave sufficient information. Robertson et al. (1951), Burger (1952), Christian & Nofziger (1952), Self et al. (1955), Gosset & Sørensen (1959), Haines et al. (1959), Hafez (1960), Zimmerman et al. (1960b), Lodge & McPherson (1961), Sørensen et al. (1961), Goode et al. (1965), O'Bannon et al. (1966), Etienne & Duée (1973), Pay & Davies (1973), Friend (1977), van Kempen (1976), Aherne et al. (1976), Friend (1977), McPherson et al. (1976) and Schilling & Schröder (1977). Overall correlation coefficients between energy intake and age and weight at puberty were calculated firstly. Age at puberty is negatively correlated with average daily gain (Table 2). This result is in agreement with data of Aherne & Price (1979), who found, within the group that came to ovulation during their trial, a negative correlation ($r = -0.569$; $P < 0.001$) between age at puberty and average daily gain. The average daily gain for pigs that reached puberty earlier, was lower than that for pigs that did not reach puberty. They used an equal feeding level for all the pigs.

Analysis of covariance was performed with age and weight at puberty as dependent and publication and feeding level (high or low) as independant variables. Age of the gilts at the start of the trial was taken as a covariable. Means of (adjusted) variables at low and high levels of energy intake are given in Table 3. Restrictedly fed gilts reached puberty significantly later (9 days) and with a significantly lower weight (19.1 kg) than gilts on a high feeding level.

For correct evaluation of data it is necessary to forecast when gilts that did not

Table 2. Overall correlation coefficients (r) of energy intake during rearing with age and weight at puberty (n is number of trials).

Correlation of	n	r	Significance (P)
Age at puberty and daily energy intake	38	−0.02	0.450
Age at puberty and average daily gain	34	−0.41	0.008
Age at puberty and weight at puberty	50	+0.57	0.001
Weight at puberty and daily energy intake	37	+0.49	0.001
Weight at puberty and average daily gain	34	+0.41	0.009
Average daily gain and daily energy intake	26	+0.62	0.001

Table 3. Relation of intake of net energy for fattening (NE_F) during rearing with age and weight at puberty (± separates mean and standard deviation).

	Low intake	High intake	Significance of difference (P)	Coefficient of variation[2] (%)
Number of trials	22	19		
Average age at start (d)	86.7 ± 27.9	85.8 ± 28.2		
Average weight at start (kg)	36.2 ± 17.5	34.8 ± 17.9		
Average daily net energy intake (MJ/d)	16.4 ± 2.6(20)[1]	25.3 ± 2.5(18)[1]		
Age at puberty (d)	211	202	< 0.06	6.8
Weight at puberty (kg)	80.0	99.1	< 0.001	7.5

[1] The number in parenthesis is number of trials in which the energy intake was well defined and not only stated as high and low.

[2] Calculated from residual mean square.

reach oestrus would do so. Van Kempen (1976) used the method of censorated data to predict the age at puberty of all the gilts in his trial (oestrus or non-oestrus). By censorated data age at puberty is assumed to be normally distributed. Age at puberty for the oestrus gilts and for all gilts differed from 4 to 11 days for the experimental groups.

The critical time for development of the uterus and ovaries of gilts is assumed to be at 70-160 days from birth (Busch, 1976). According to Günther (1974), the development of the different organs follows certain rules. First nervous system and the important organs like heart, liver, kidneys and lungs develop. Then the muscles, bones, fat tissue and udder follow. Lastly energy from the ration goes to the reproductive organs. According to this hypothesis a deficiency of energy during rearing would probably first be seen in a decreased fertility. For reaching puberty age is more important than weight. Gilts which are very thin at a certain age will not reach puberty (McCance & Widdowson, 1974). At the other side some investigations (left column in Table 1) showed a reduction in age at puberty with feed restriction during rearing. These two phenomena suggest that there are minimum and maximum fat contents of the body required which act as a threshold for reaching puberty. Between these limits age is the determining factor. Perhaps pigs with thin backfat have relatively more internal fat. In human females, there is a difference in fat deposition between early and late sexual maturation (Frisch, 1975). Frisch mentioned three possibilities: (1) storage of oestrogen in fat depots affects blood levels of oestrogen, or other steroids or their secretion rates; (2) oestrogen metabolism may be influenced by factors in fat metabolism, including thyroid hormones; (3) fat content is important in regulating hypothalamus.

Protein restriction

For the effect of protein restriction during (part of) rearing, there is more agreement in the literature than about energy restriction (Table 4). Except for Robertson et al. (1951) and Naber et al. (1972), all the authors found no effect or an unfavourable effect of protein restriction on age at puberty. The protein given by Naber et al. (1972) had, however, an increased lysine content. More important than protein content would be the content of amino acids. Normally the first limiting amino acid for pigs is lysine. There is some evidence that only a severe inbalance in essential amino acids may delay the onset of puberty in gilts (Friend, 1973).

Number of ovulations in gilts

Relation of energy intake during rearing with ovulation rate

Generally number of corpora lutea is used as measure of number of ovulations. Mistakes are made when a fertilized ovum resulted in two or more embryos (polyembryony) or a follicle gives two or more ova (polyovuly). Polyembryony results in monozygotic (identical) twins. Among 80 pregnant sows Pomeroy (1960) found 2 with more embryos than corpora lutea. Table 5 gives the relation between feeding level during rearing and ovulation rate. A high feeding level during rearing generally increased number of ovulations.

For statistical evaluation of ovulation, publications of the following authors were studied: Robertson et al. (1951), Self et al. (1955), Haines et al. (1959), Gosset &

Table 4. Influence of protein restriction during rearing on age at puberty. There was calculated whether age at puberty was significantly increased or decreased by protein restriction. If the effect was not significant, trials with 5 days or more difference were added to the trials with a significant effect. A decrease in age at puberty was taken as favourable and an increase as unfavourable.

Authors who found a favourable effect	Authors who found no effect	Authors who found an unfavourable effect
Robertson et al. (1951)*	Etienne & Legault (1974)	Holness (1972)**
Naber et al. (1972)**	Friend (1976)	Cunningham et al. (1974)**
	Friend (1977)	Duée & Etienne (1974)
		Duée (1977)
		Jones & Maxwell (1974)
		Wahlstrom & Libal (1977)*

Significant difference: * $P < 0.05$; ** $P < 0.01$

Table 5. Influence of a high feeding level during rearing on the number of ovulations in gilts. If the number of ovulations is increased by 0.5 ovum, the effect is described as favourable.

Favourable effect		No effect	
Robertson et al.	(1951)*	Goode et al.	(1965)
Christian & Nofziger	(1951)*		
Self et al.	(1955)**		
Haines et al.	(1959)**		
Gosset & Sørensen	(1959)		
Hafez	(1960)		
Sørensen et al.	(1961)**		
O'Bannon et al.	(1966)*		
Bazer et al.	(1968)		
Frobish & Gerrits	(1969)		
Frobish	(1970)		
Brooks et al.	(1972)*		
Etienne & Duée	(1973)*		
Duée & Etienne	(1974)*		
van Kempen	(1976)		
van de Kerk & Elsinghorst	(1976)		

Significant difference: * $P < 0.05$; ** $P < 0.01$.

Sørensen (1959), Hafez (1960), Sørensen et al. (1961), Goode et al. (1965), O'Bannon et al. (1966), Christenson & Zimmerman (1966), Bazer et al. (1968), Frobish & Gerrits (1969), Frobish (1970), Brooks et al. (1972), Etienne & Duée (1973) and van Kempen (1976). Normally number of ovaluations increased during the first three times of oestrus after reaching puberty. So oestrus number (first, second or third) was used as a covariable. Means of (adjusted) variables at low and high levels of energy intake are given in Table 6. Restricted energy intake during rearing resulted in significantly fewer ovulations than a high feeding level. Except for two publications, the low and high feeding levels fell into separate groups with slight overlap (Fig. 1). Anderson & Melampy (1972) reviewed the results of 22 trials in which gilts received different intakes of net energy for 1-3 months before ovulation. The 'full-fed' gilts (about 25.1 MJ/d) had 1.2 ovulations more than the restrictedly fed gilts (about 16.6 MJ/d).

Table 6. Number of ovulations after low and high energy intake during rearing (± separates mean and standard deviation).

	Number of trials	Intake of energy (MJ/d)	Number of ovulations[1]
Low	21	15.6 ± 3.4	11.8*
High	21	24.9 ± 4.0	13.2*

* Significant difference (< 0.001).

[1] Coefficient of variation (calculated from residual mean square) was 8.4 %.

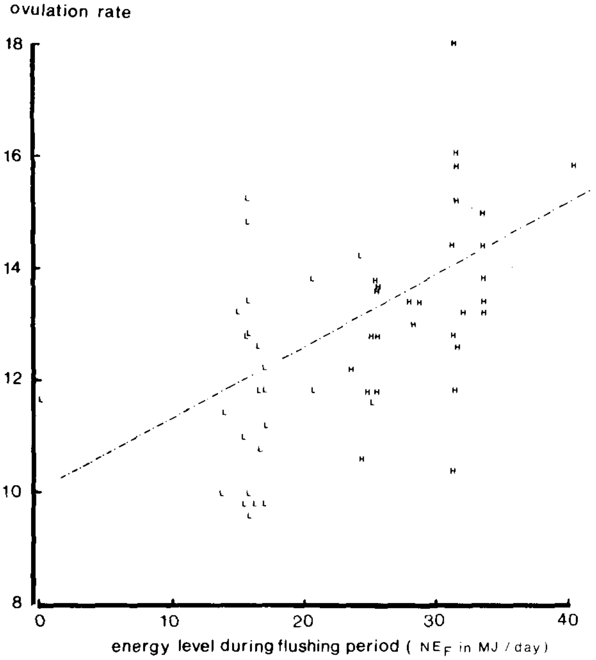

Fig. 1. Relation between energy level during rearing (x) and ovulation rate (y). $Y = 0.15x + 9.41$; $r = 0.50$; $n = 44$; $P < 0.001$.

Relation of energy intake before oestrus with number of ovulations

A high feeding level before oestrus usually caused a significant improvement in number of ovulations (Table 7). A high feeding level on the day of oestrus had a positive effect on the number of corpora lutea; on the day after oestrus it had no effect. The increase with flushing on the day of mating could be due to rupture or regression of immature follicles. The number of corpora lutea increased, but not the number of ovulations (Brooks & Cooper, 1972).

For the statistical evaluation we used results from the following authors: Self et al. (1955), Zimmerman et al. (1960a), McGillivray et al. (1962, 1963), Rigor et al. (1963), Short et al. (1963), Schultz et al. (1965), Kirkpatrick et al. (1967a, 1976b), Bazer et al. (1968), Clawson (1969), Frobish & Gerrits (1969), Frobish (1970), Naber & Zimmerman (1971, 1972), Brooks et al. (1972), Clark et al. (1972, 1973), Edey et al. (1972), Staigmiller et al. (1972), Moore et al. (1973), Daily et al. (1975), van Kempen (1976) and Emerson & Henricks (1977). First we calculated the general correlation coefficient (r) and linear regression of average rate of intake of net energy during flushing with number of ovulations (Fig. 2). By covariance analysis with the factors high and normal energy intake and publication, we corrected for difference in duration of flushing. The average duration of flushing was 13.1 ± 5.6 days. In Table 8 the means of the traits with and without flushing are given. Flushing of gilts

Table 7. Influence of flushing on the number of ovulations in gilts. If the number of ovulations is increased or decreased by 0.5 ovum, the effect is described as favourable or unfavourable, respectively.

Period of high feeding level	Favourable effect		No (N) or unfavourable (U) effect	
4-21 days before oestrus	Self et al.	(1955)**	van Kempen	(1976) (U)
	Zimmerman et al.	(1958)**	van de Kerk & Elsinghorst	(1976) (U)
	Zimmerman et al.	(1960a)		
	McGillivray et al.	(1962)		
	McGillivray et al.	(1963)		
	Rigor et al.	(1963)**		
	Short et al.	(1963)*		
	Schultz et al.	(1965)**		
	Schultz et al.	(1966)*		
	Kirkpatrick et al.	(1967a)*		
	Kirkpatrick et al.	(1967b)*		
	Bazer et al.	(1968)*		
	Moore et al.	(1971)**		
	Naber & Zimmerman	(1971)*		
	Brooks et al.	(1972)		
	Clark et al.	(1972)**		
	Dailey et al.	(1972)		
	Edey et al.	(1972)*		
	Naber & Zimmerman	(1972)**		
	Staigmiller et al.	(1972)		
	Moore et al.	(1973)**		
	Dailey et al.	(1975a)		
	Dailey et al.	(1975b)		
	Emerson & Henricks	(1977)		
Day of oestrus	Lodge & Hardy	(1968)*	Te Brake	(1971) cited by
	Moore et al.	(1971)*	Brooks & Cooper	(1972) (N)
	Brooks et al.	(1972)*	Brooks & Cole	(1971) (N)
	Cooper et al.	(1973)*	Naber & Zimmerman	(1971) (N)
			Libal et al.	(1972) (N)
			Moore et al.	(1973) (N)
Day after oestrus			Libal & Wahlstrom	(1970)
			cited by Rerat & Duée	(1975)
			Brooks et al.	(1972) (N)
			Staigmiller & First	(1973) (U)

Significant difference: * $P < 0.05$; ** $P < 0.01$.

has a positive effect on number of ovulations (+ 1.9). The extra energy intake of the flushed gilts was on avered 82 % more than of the unflushed gilts. Anderson & Melampy (1972) also found in their literature review a positive effect of extra energy intake before oestrus on number of ovulations. From various investigations optimum duration of the high-energy regime seemed to be 11-14 days before expected data of oestrus or mating. At a low level of feeding ovulation rate in the gilt is under genetic

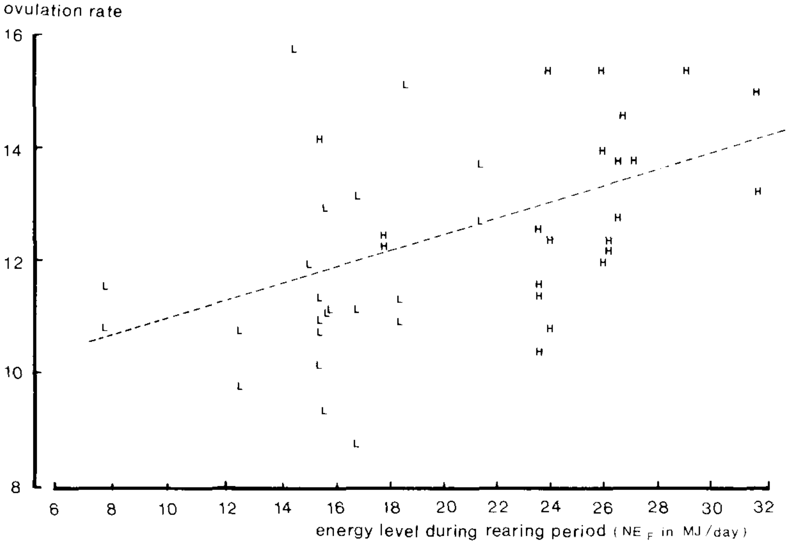

Fig. 2. Relation between energy level shortly before oestrus (x) and ovulation rate (y). $y = 0.12x + 9.82$; $r = 0.54$; $n = 53$; $P \ll 0.001$.

control. Short-term increases in dietary energy above maintenance increase number of ovulations (Brooks & Coole, 1974). The favourable effect depends mainly on energy.

There were too few trials on flushing on the day of oestrus for statistical analysis.

Relation of feeding level during rearing with conception rate

There is no agreement in the literature on the influence of nutrition on conception rate (proportion of gilts becoming pregnant). Some research workers (Christian & Nofziger, 1952; McGillivray et al., 1963; Myers & Speer, 1963; Brooks et al., 1975; Etienne et al., 1976; Varley & Cole, 1976) found no clear effect of feeding level on conception rate. Others (King & Young, 1957; Lodge & McPherson, 1961) found a higher conception rate for pigs on a high feeding scheme than in controls. Conception rate was studied for different sequences of feeding level during rearing and

Table 8. Influence of flushing on number of ovulations (± separates mean and standard deviation).

	Number of trials	Intake of net energy (MJ/d)	Number of ovulations[2]
Low energy intake (no flushing)	30	16.6 ± 4.5 (25)[1]	11.8*
High energy intake (flushing)	36	30.2 ± 4.0 (28)	13.7*

* Significant difference ($P < 0.001$).

[1] In parenthesis the number of trials in which energy intake was well defined and not only stated as high and low.

[2] Coefficient of variation (calculated from residual mean square) was 8.8 %.

Table 9. Conception rates for different sequences of feeding levels during rearing. The combinations of feeding levels were: low till mating (LL), high till mating (HH) and low during rearing with flushing afterwards (LH).

Combination of feeding levels	Number of trials	Mean conception rate (%)[1]
LL	12	82.6
LH	6	88.0
HH	8	80.5

[1] Coefficient of variation (calculated from residual mean square) was 14.3 %.

flushing. Data from the following authors were used: Gosset & Sørensen (1959), Lodge & McPherson (1961), O'Brannon et al. (1966), Schultz et al. (1966), Bazer et al. (1968), Lodge & Hardy (1968), Frobish & Gerrits (1969), Cooper et al. (1973), Moore et al. (1973), Pay & Davies (1973), van Kempen (1976) and McPherson et al. (1977). The average conception rate in 26 trials was 83.2 %. A restricted feeding level during rearing followed by a flushing gave a higher conception rate than a continuously low or high feeding level (Table 9).

Relation of feeding level with embryonic mortality

According to a literature review of Te Brake (1975) prenatal mortality may be estimated at about 40 %. Most prenatal losses occur in the embryonic period, mainly before the 25th day after mating; during the foetal period (after 35 days of pregnancy; Wrathall, 1975), the mortality is less, presumably no more than 10 % (Te Brake, 1975). Critical period for embryonic survival are during distribution in the uterus (11-13 d after mating), at implantation (13-23 d after mating) and during organ development (Hafez, 1959; Anderson, 1974). The greatest embryonic loss in farmstock seems to be at implantation, in contrast to the situation in rabbits, rats and mice where there are two peaks of losses, before and after implantation. The process of implantation is critical for correct balance of hormones; conditions suitable for blastocyst growth may not be suitable for implantation (Lamming, 1969). Many factors influence embryonic survival. According to Webel & Dziuk (1974), embryonic mortality, first 30 days of pregnancy, does not result from lac of uterine capacity. They mentioned as possible causes for the high embryonic mortality: mistakes at fertilization or genetic aberrations.

A high energy intake by pregnant gilts has unfavourable effects like:

- increased embryonic mortality during early pregnancy
- more complications at farrowing
- more cases of low milk production
- a tendency for more fertility problems (Schneider & Bronsch, 1975).

After flushing, it is advisable to reduce feed or energy level because of the increased chance of embryonic mortality (Robertson et al., 1951; Christian & Nofziger, 1952, Self et al., 1966; Gosset & Sørensen, 1959; Haines et al., 1959; Hanly, 1961; Sørensen et al., 1961; Dimov, 1963; Boyd, 1965; Goode et al., 1965; Tassel, 1967; Dutt & Chaney, 1969; Frobish & Gerrits, 1969; Lamming, 1969; Vanschoubroek, 1969; Englisch et al., 1971; Scofield, 1972; van Kempen, 1973, 1976; Wrathall, 1975; Hansel & McEntee, 1977).

An energy deficiency during early pregnancy can result in:
- embryonic or foetal death followed by abortion or resorption
- malformations of embryo or foetus
- delay in development and growth of the foetus (Lamming, 1969).

For the statistical evaluation, trials of the following authors were screened: Robertson et al. (1951), Self et al. (1955), Haines et al. (1959), Gosset & Sørensen (1959), Hafez (1960), Sørensen et al. (1961), Short et al. (1963), McGillivray et al. (1963), Goode et al. (1965), O'Bannon et al. (1966), Schultz et al. (1965, 1966), Christenson & Zimmerman (1966), Bazer et al. (1968), Frobish & Gerrits (1969), Libal & Wahlstrom (1970), Frobish (1970), Naber et al. (1971), Brooks et al. (1972), Cooper et al. (1973), Etienne & Duée (1973), Moore et al. (1973), van Kempen (1976) and Emerson & Henricks (1977). The following variables were taken: number of days of pregnancy at slaughter; intake of net energy during rearing, flushing and pregnancy until slaughtering; number of embryos alive for the pregnant gilts; embryonic survival (number of embryos divided by number of corpora lutea) and publications. In total, 24 trials were screened. Generally a higher level of energy during rearing resulted in a higher embryonic mortality (Table 10). The higher feeding level during flushing resulted in more embryos per gilt. The average duration of pregnancy at the time of slaughter was 28.0 ± 5.4 days for the gilts. When the duration of pregnancy was longer, the embryonic mortality may be higher and the number of embryos alive per gilt smaller. So we used duration of pregnancy at slaughter as covariable in the analysis of variance. A high feeding level in the different periods always gave a higher embryonic mortality (Table 11). Higher embryonic mortality can result from a higher ovulation rate at the high energy level.

As yet the periods under study have been considered separately, but now they will be studied in relation to one other. A higher energy level during rearing and flushing seems to increase the number of ova shed. Effects of flushing may be influenced by feeding level in the preceding period (carry-over effects). With three periods studied (rearing, flushing and early pregnancy) and two energy levels, there are 2^3 possible combinations. Not all these combinations have been studied. Only 3 combinations (LLL, LHL and HHH) have been studied often (Table 12). We used covariance analyses only for these 3 combinations with duration of pregnancy at slaughter as covariable. A constant low energy level gave low embryonic mortality, but fewer ova were shed (Table 13). The calculated average number of ova shed was 12.6, 13.9

Table 10. Correlation coefficients (r) of intake of net energy for fattening during several periods with embryonic survival and number of embryos alive.

Period	Number of trials	Number of embryos alive per gilt	Embryonic survival (%)
Rearing	55	−0.10 (P = 0.23)	−0.27 (P = 0.02)
Flushing	61	0.22 (P = 0.04)	−0.09 (P = 0.24)
Early pregnancy	59	0.07 (P = 0.29)	−0.06 (P = 0.34)

Table 11. Difference between high and low feeding levels during different periods for reproduction traits (± separates mean and standard deviation).

Period	Number of trials	Feeding level	Intake of net energy (MJ/d)[1]	Number of embryos alive per gilt[2]	Embryonic survival (%)[2]
Rearing	19	high (H)	26.3 ± 3.1 (17)	9.8	69.7
	46	low (L)	16.8 ± 3.0 (38)	10.0	77.5
Difference (H-L)	–	–	9.5	−0.2 (P = 0.72)	−7.8 (P = 0.01)
Flushing	36	high	28.4 ± 5.4 (33)	10.1	73.2
	31	low	15.9 ± 3.3 (28)	9.7	78.3
Difference (H-L)	–	–	12.5	+0.4 (P = 0.19)	−5.1 (P = 0.04)
Early	22	high	27.3 ± 3.7 (22)	9.9	72.1
pregnancy	45	low	16.9 ± 3.1 (37)	10.0	77.2
Difference (H-L)	–	–	10.4	−0.1 (P = 0.84)	−5.1 (P = 0.08)

[1] In parenthesis the number of trials in which the energy intake was well defined and not only stated as high and low.

[2] Coefficients of variation (calculated from residual mean square) of number of embryos alive per gilt and embryonic survival were 14.4, 14.0, 14.2 and 12.4, 12.6, 12.8 for rearing, flushing and early pregnancy respectively.

Table 12. Possible combinations of period of feeding and energy level (high = H and low = L).

Rearing period	Flushing period	Early pregnancy	Number of trials
L	L	L	26
L	L	H	3
L	H	L	14
L	H	H	3
H	L	L	1
H	L	H	0
H	H	L	3
H	H	H	15

and 14.0 for the combination LLL, LHL and HHH, respectively. A high constant level of energy was related to high embryonic mortality and to large number of ova shed. But the number of embryos per gilt was nearly the same as at constant low energy levels. The combination LHL seems to be most favourable in the short run. Though high-energy diets before mating increase ovulation, continuation of these dietary schemes causes greater loss of embryos (Anderson & Melampy, 1972).

Embryonic survival did not differ significantly for pigs on different levels of protein during rearing or pregnancy (Svajger et al., 1972; Duée & Etienne, 1974; Jones & Maxwell, 1974; Hammel et al., 1976; Duée, 1977; Wahlstrom & Libal, 1977). Protein requirements during pregnancy seems of minor significance compared with

Table 13. Influence of energy level on two reproduction characteristics for the three most frequently studied combinations of treatments. Mean values in the same row bearing a common superscript are not different (ab $P < 0.05$) (± separates mean and standard deviation).

Sequence of treatment	LLL	LHL	HHH	Coefficient of variation (%)[2]
Duration of pregnancy (d)	28.0 ± 5.6	28.1 ± 5.6	29.1 ± 6.8	
Number of treatments (n)	26	14	15	
Intake of net energy[1] (MJ/d)				
– rearing	16.4 ± 3.0 (22)	17.9 ± 3.5 (10)	27.0 ± 2.5 (13)	
– flushing	16.2 ± 3.1 (23)	32.6 ± 5.8 (11)	27.0 ± 2.4 (15)	
– pregnancy	17.0 ± 2.4 (22)	18.1 ± 3.4 (11)	27.4 ± 2.5 (15)	
Number of embryos alive per gilt	9.90	10.75	9.84	12.4
Embryonic survival (%)	78.7^{a}	77.6^{a}	70.3^{b}	11.8

[1] In parenthesis the number of trials in which the energy intake was well defined and not only stated as high and low.

[2] Calculated from residual mean square.

energy (van Kempen, 1973). Pregnant sows will still grow on a maintenance scheme for non-pregnant sows. Explanations for this phenomenon are:

- an increased moisture retention of tissues
- a decreased maintenance requirement
- an increased utilization of nutrients (Busch, 1970).

Acknowledgements

The authors wish to thank Dr Ir M. W. A. Verstegen for the valuable comments and Mr J. C. Rigg for checking the English.

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