Studies on the energy metabolism of the pregnant sow

1. Uterus and mammary tissue development

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(*Received 1 February 1984 – Accepted 7 September 1984*)

1. Twenty-six gilts were used in an experiment to study the effects of level of feed intake on the growth and chemical composition of the gravid uterus and mammary tissue at several stages of gestation. The animals were given either 1·8 or 2·5 kg feed/d (20 or 30 MJ metabolizable energy (ME) respectively) and were slaughtered at intervals between days 40 and 110 of gestation. The gravid uterus was dissected into fetal, placental, fluid and empty uterus components. From day 70 of gestation the mammary tissue was also dissected. The fresh weight and dry matter (DM), energy and nitrogen contents of the various tissues were determined.

2. (a) With the exception of the fluid component, there was a significant increase ($P < 0·01$) in the fresh weight of each tissue with both stage of gestation and level of feeding. At comparable litter sizes the total weight of the fetuses in late gestation was 16% higher with the higher feed intake. (b) The DM content of the individual uterine tissues increased significantly ($P < 0·01$) with increase in stage of gestation so that the mean DM content of the gravid uterus increased from 74·6 g/kg at day 50 to 103·1 and 159·0 g/kg at days 90 and 110 of gestation respectively. (c) Neither stage of gestation nor feeding level influenced the respective energy contents of the individual uterine tissues, when expressed per g DM. The mean energy content of the total gravid uterus was 19·5 kJ/g DM. (d) The N content (g/g fresh weight) of the tissues increased with stage of gestation and was generally higher at the higher feeding level. The mean N contents (g/g DM) of the fetal, placental, fluid and empty uterine tissues were 0·090, 0·101, 0·098 and 0·128 respectively.

3. The mammary tissue was the most variable of all the tissues investigated. Whereas the fresh weight and N content increased with stage of gestation, both the DM and energy content decreased.

4. Gompertz equations were fitted to describe the effects of stage of gestation, level of feed intake and litter size on the fresh weight and chemical content of the individual uterine tissues, total gravid uterus and mammary tissue. The use of these equations for calculating the nutrient requirements of pregnancy is demonstrated.

5. It was calculated that between days 50 and 110 of gestation the ME requirement for reproduction increased from 3 to 12% of maternal energy intake. The calculated requirement for protein was from 7 to 41% of maternal dietary protein intake respectively.

In order to predict the nutrient requirements throughout pregnancy, it is necessary to know the changes which occur in both the reproductive and maternal tissues. In the past, the nutrient requirements of the pregnant sow have been based on an empirical approach by which reproductive characteristics such as sow-weight gain, litter size and average birth weight of the piglets have been assessed in relation to various nutritional inputs (e.g. Agricultural Research Council, 1967). More recent estimates have used a factorial approach by which the respective rates of tissue deposition have been estimated and, on the basis of an assumed efficiency, the nutrient requirements have been calculated (Vanschoubroek & Van Spaendonck, 1973; Agricultural Research Council, 1981). The information which forms the basis of these calculations has been taken from a variety of experiments conducted

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with animals of different breeds, of differing nutritional states and under various environmental and management systems. These factors could influence the rate and efficiency of tissue deposition. In addition, the information pertaining to the weight and chemical composition of the reproductive tissue at different stages of gestation is limited, being chiefly restricted to the results of De Villiers *et al.* (1958), Pomeroy (1960), Moustgaard (1962) and Kemm & Ras (1976). These results describe only the extent to which the fetal and other reproductive tissues change with duration of gestation and do not take into account the variation associated with the level of feed intake, litter size or other factors influencing fetal development. More extensive information concerning prenatal growth and composition of the reproductive tissue is therefore required to provide a reliable base on which the nutrient requirements of the pig can be calculated during pregnancy.

The present experiments were undertaken in an attempt to provide this information by studying the weight and chemical composition of the fetus, placenta, fetal fluids, uterus and mammary tissue of the sow at several stages of gestation when fed at different levels. It was also possible to examine the effects of variations in litter size. Equations were derived from this information to describe the extent to which the growth and development of the uterine tissues changed during gestation, thus providing more extensive information on which to base the calculation of the nutrient requirements of the pregnant sow.

MATERIALS AND METHODS

Animals

The animals were of the Large White breed from the Institute's herd of enzootic–pneumonia-free animals. They were selected in groups of four animals, each group comprising only litter sisters. Before their first oestrus cycle, at approximately 4 months of age, the animals were transferred to a straw-bedded sow house equipped with individual feeding facilities. In this building the animals were in close contact with more-mature breeding sows and boars. At the third oestrus period two of the four animals were mated on two successive days with the second day being regarded as the first day of gestation (day 1). The remaining two animals in the group were kept as non-pregnant controls. All animals remained in the sow house until required for experimentation.

Experimental design

The experiments were designed in a 2×3 factorial arrangement involving two levels of feeding at three separate stages of gestation. The feeding levels, which were applied immediately following mating and which remained constant throughout gestation, were 1·8 (low) and 2·5 (high) kg feed/d. The periods of gestation within which the animals were investigated were 40–60 d (early), 60–80 d (middle) and 90–110 d (late). Four pregnant gilts, two animals from each of two groups, were investigated within each treatment, with the exception of the late–high treatment for which six pregnant animals were investigated. The remaining four non-pregnant litter sisters, which were of comparable age at each stage of gestation, acted as controls. As there were six combinations of feeding level and stage of gestation, the experiment involved a total of fifty animals, twenty-six pregnant and twenty-four non-pregnant.

Plan of experiments

Until mating, all animals were given 2·0 kg feed/d. Immediately following mating the feed intake of the animals was adjusted to that of the experimental treatment. In the sow house all animals were weighed at weekly intervals. At 4 weeks before the appropriate stage of gestation, the animals were moved into a temperature-controlled farrowing house (20 (SE 1)°) and accommodated in individual farrowing pens. This period served to habituate the animals to the experimental conditions and protocol. Following habituation the animals

Table 1. *The chemical composition of the feed (g/kg dry matter (DM))*
(Mean values with their standard errors)

	Mean	SE
DM (g/kg)	885	7
Crude protein (nitrogen × 6·25)	183	11
Crude fibre	57	0·8
Diethyl-ether extract	22	0·9
Ash	68	1
Silicon-free ash	57	0·7
Calcium	9·8	0·2
Phosphorus	6·7	0·1
Potassium	10·4	0·1
Magnesium	2·6	0·2
Sodium	1·8	0·05
Copper (mg/kg)	48	3
Zinc (mg/kg)	143	3
Manganese (mg/kg)	92	3
Gross energy (MJ/kg DM)	18·0	1·0
Metabolizable energy (MJ/kg DM)	13·3	0·8

were removed to a specially-designed heat-sink calorimeter (Close *et al.* 1978) maintained at 20 (SE 0·5)°. Each animal remained in the calorimeter for 7 d when its heat loss and energy and nitrogen balances were determined (Close *et al.* 1985). At the end of the calorimetric period the animals, both pregnant and control, were weighed and slaughtered and their uterus and mammary tracts removed for subsequent chemical analysis.

Nutrition

The animals were given a sow diet comprising barley, wheat, maize meal and soya-bean meal with added vitamin and mineral supplements. Samples of feed were taken weekly throughout the experiment and analysed for their chemical composition. This is shown in Table 1. The feed was offered in pelleted form and given in equal amounts at 09.00 and 16.00 hours each day thus providing 20 and 30 MJ ME/d on the low and high intakes respectively. The animals always had access to water.

Slaughter procedure and dissection of the reproductive tissue

The gravid uterus was removed from the animal immediately following slaughter. The uterus was severed at the cervix, removed intact and weighed. It was then placed on a large dissecting tray and each uterine horn was fully extended to aid dissection into fetal, placental, fluid and uterine tissue components. A longitudinal incision was made along each uterine horn and each fetus was individually removed, its sex and position within the uterine horn recorded, and then weighed. All fetuses were subsequently bulked and deep-frozen at −20°. The placental material from each uterine horn was also removed, weighed, bulked and deep-frozen. The remaining empty uterus was weighed and deep-frozen, having previously been washed with water and dried. The total fluids associated with the gravid uterus remained in the dissecting tray. The contents of the tray were transferred to a plastic bin and the tray was washed with water. The uterine fluids and washings were weighed and thoroughly mixed and a sample taken for subsequent chemical analysis. The weight of fluids *per se* was determined from the differences between that of the total gravid uterus and that of its fetal, placental and empty uterine components. Following the gravid uterus, the mammary tissue was removed from its surrounding connective tissue, weighed and also deep-frozen until required for analysis.

For the non-pregnant animals, the intact uterus was removed, weighed and deep-frozen.

Chemical analysis

With the exception of the heat of combustion, all chemical analysis was carried out on the fresh material. Homogeneous samples of each of the various tissues were obtained by chopping and mincing the frozen material through a 2 mm plate. The resulting material was thoroughly mixed and sampled. The sample was then allowed to thaw, again thoroughly mixed and a portion taken for subsequent chemical analysis.

DM content of the various tissues was determined following freeze-drying. The heat of combustion was determined on a sample of the freeze-dried material, following ignition in an adiabatic bomb calorimeter. N content was determined on samples of the freshly-thawed material following digestion according to the Kjeldahl method. Protein content was calculated on the basis that the N content of protein is 160 g/kg (N × 6·25). The energy value was taken to be 23·8 kJ/g protein (Brouwer, 1965).

Statistical analysis

Because some of the variables, for example litter size, could not be controlled, direct comparison between the mean responses of the different treatments was not feasible. The only appropriate method was the use of regression analysis to fit equations which would relate the various indices measured to functions of the stage of gestation and any additional variable found to be of importance. For this purpose, the basic criterion was that the selected model should have the highest degree of correlation and the smallest residual sum of squares in the logarithmic scale, since variability was approximately constant in that scale, with no coefficients included which were not generally significantly different from zero. It was also important that the function and the rate of change of the function should have an appropriate qualitative form over the ranges of gestation of interest. A further criterion was that the difference between the sum of the individually-predicted uterine components and that derived from the model for total gravid uterus should be as small as possible for both the absolute values and their rates of change. The model which best fulfilled these criteria was the logarithmic form of the Gompertz equation and this model was used to describe the dependence of the uterine components on the stage of gestation with additional terms to allow for variation associated with litter size and feed intake. The model was, therefore:

$$\mathrm{Log_e}\, y = \mathrm{A} + \mathrm{B} \exp(-\mathrm{k}(t-45)) + \mathrm{C}ft + \mathrm{D}n, \qquad (1)$$

where y is the variable under investigation, t is the stage of gestation (d), f is the metabolizable energy (ME) intake (MJ/d), n is the number of viable fetuses and A, B, C, D and k are constants. The value of t in eqn (1) did not extend below 45 d since this was the earliest stage at which the animals were investigated. Correlations due to pairs of animals being selected from the same litter were ignored. Although it was impossible to control the number of fetuses, there was a strong correlation between energy intake and litter size so that the average litter size for those animals receiving the high intake was different from those receiving the low intake. Thus the effects of litter size and level of feed intake could not be completely separated and both variables were included in the model even when they were clearly non-significant. The model included the term ft rather than f since the cumulative feed intake up to the time of measurement was considered to be more directly related to the variable under investigation. Body-weight of the sow produced no significant effect and was not included as a variable in the computations.

For the calculations of the fresh weight and the DM, energy and N contents of the fetus, placenta, empty uterus and total gravid uterus, the model was that described in eqn (1). For the fluid component, the use of eqn (1) did not reflect the changes which occured in its fresh weight and chemical composition. A quadratic function of the form:

$$\mathrm{Log_e}\, y = \mathrm{A} + \mathrm{B}t + \mathrm{C}t^2 + \mathrm{D}n \qquad (2)$$

was found most appropriate, with y being the fresh weight, DM, energy or N content of the fluids, t the stage of gestation (d) and n the number of fetuses. Level of energy intake had no significant effect ($P > 0{\cdot}05$) on the total weight of the fluids or their chemical composition and was therefore not included in eqn (2).

Of all the tissues investigated, that of mammary tissue varied most, both within and between treatments. The results showed an exponential dependence on stage of gestation. There was a significant response due to energy intake but not for litter size, and the latter was excluded from the analysis. The model was therefore:

$$\text{Log}_e y = A + B \exp(-k(t-45)) + Cf, \quad (3)$$

where y is the fresh weight, DM, energy or N content of the mammary tissue, t is the stage of gestation (d) and f is the ME intake (MJ/d).

The various regression equations have been used to predict the total fresh weight and chemical composition of the uterine and mammary tissues at several stages of gestation in relation to both ME intake and litter size.

RESULTS

Control animals

At each comparable stage of gestation, the weight gain of the control animals was always less than that of their pregnant litter sisters. The daily weight gain of the pregnant animals varied between 0·38 (SE 0·04) and 0·64 (SE 0·02) kg depending on the stage of gestation and level of feeding; the corresponding range for the control animals was 0·16 (SE 0·05) to 0·44 (SE 0·08) kg/d.

There was no significant effect of body-weight or level of feed intake ($P > 0{\cdot}05$) on either the fresh weight or chemical composition of the non-pregnant uterus. The mean (with SE) chemical composition was 836 (44) g fresh weight, 162 (2·7) g DM/kg, 21·28 (0·12) kJ/g DM and 20·75 (0·52) g N/kg. The non-gravid uterus contained 135·4 g DM, 17·34 g N, and had a heat of combustion of 2882 kJ. If the heat of combustion is assumed to be derived from both protein (23·8 kJ/g) and fat (39·7 kJ/g), then the uterus contained 7·6 g fat. The mean fresh weight of the non-gravid uterus was 47% of that of the empty gravid uterus at day 52 of gestation (mean of low and high feeding levels) and although the energy content per g DM was similar, the non-gravid uterus had a significantly higher ($P < 0{\cdot}05$) DM and N content.

Pregnant animals

Reproductive efficiency. One animal produced only five viable piglets and another refused feed during the calorimetric period; the results of these were excluded from the analysis. The remaining animals performed satisfactorily, as can be judged from the increase in body-weight between mating and slaughter and the number of viable fetuses at each stage of gestation (Table 2). As all animals had been fed similarly before mating it was not expected that the previous nutritional history would have influenced litter size. Within each uterine horn there were large variations in fetal body-weight depending on the position of attachment and sex. The largest fetus was always found near the ovaries and the smallest in close proximity to the cervix. Male fetuses were approximately 10% heavier than females, and this was independent of the site of attachment within the uterus.

Uterine components

Weight. The mean weights of the tissues comprising the gravid uterus are presented in Table 3. In six of the pregnant gilts, individual fetuses were found in various stages of degeneration. These were of an earlier gestational age than their litter-mates as determined

Table 2. *The influence of level of energy intake on the reproductive performance of pregnant gilts at several stages of gestation*

(Mean values with their standard errors)

Wt at mating (kg)		Stage of gestation (d)		Wt at slaughter (kg)		No. of viable fetuses		Total uterine wt (kg)	
Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
				Low intake (20 MJ ME/d)					
105·1	6	51	1	124·8	6	11	1	6·53	1·24
116·8	6	79	1	147·1	2	10	0	15·20	1·50
114·1	3	102	3	155·7	1	12	1	20·18	0·96
				High intake (30 MJ ME/d)					
113·9	6	53	2	142·2	3	13	1	8·52	1·11
104·1	2	72	2	148·5	4	11	2	14·08	1·97
139·5	6	103	2	203·3	5	13	1	24·53	0·81

ME, metabolizable energy.

Table 3. *The weight (g) of the uterine tissues of pregnant gilts in relation to stage of gestation and level of energy intake*

(Mean values with their standard errors)

Stage of gestation (d)		Fetus		Placenta		Fluids		Empty uterus	
Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
				Low intake (20 MJ ME/d)					
51	1	572	123	2018	453	2320	566	1615	195
79	1	4554	562	3161	198	5232	822	2253	105
102	3	9918	741	3877	390	3722	320	2663	272
				High intake (30 MJ ME/d)					
53	2	856	131	2366	181	3320	629	1975	197
72	2	3338	508	3085	346	5482	1238	2119	230
103	2	12781	455	4906	315	3370	366	3433	198

ME, metabolizable energy.

Regression equations relating the weight (W; g) of the individual uterine tissues and total gravid uterus to stage of gestation (t; d), no. of fetuses (n) and level of energy intake (f; MJ ME/d):

Fetus: $\log_e W = 8{\cdot}72962 - 4{\cdot}07466 \exp(-0{\cdot}03318\,(t-45)) + 0{\cdot}000154\,ft + 0{\cdot}06774\,n$ (R^2 0·99),

Placenta: $\log_e W = 7{\cdot}02746 - 0{\cdot}95164 \exp(-0{\cdot}06879\,(t-45)) + 0{\cdot}000085\,ft + 0{\cdot}09335\,n$ (R^2 0·85),

Fluids: $\log_e W = -0{\cdot}26360 + 0{\cdot}18805\,t - 0{\cdot}001189\,t^2 + 0{\cdot}13194\,n$ (R^2 0·79),

Empty uterus: $\log_e W = 6{\cdot}81760 - 0{\cdot}60473 \exp(-0{\cdot}04610\,(t-45)) + 0{\cdot}000111\,ft + 0{\cdot}07790\,n$ (R^2 0·82),

Total gravid uterus: $\log_e W = 8{\cdot}74519 - 1{\cdot}59844 \exp(-0{\cdot}05407\,(t-45)) + 0{\cdot}000060\,ft + 0{\cdot}09745\,n$ (R^2 0·96).

from the characterization of the appendicular skeletons of fetuses of known age. (Wrathall *et al.* 1974). These were not included in the analysis of the results.

An increase in gestational age caused a significant increase in the weight of the individual uterine components ($P < 0{\cdot}01$). Except for the values determined at the high feeding level in mid-gestation, increasing feed intake was also associated with an increase in weight. At this stage the weights were lower than anticipated, and may have been due to the increased

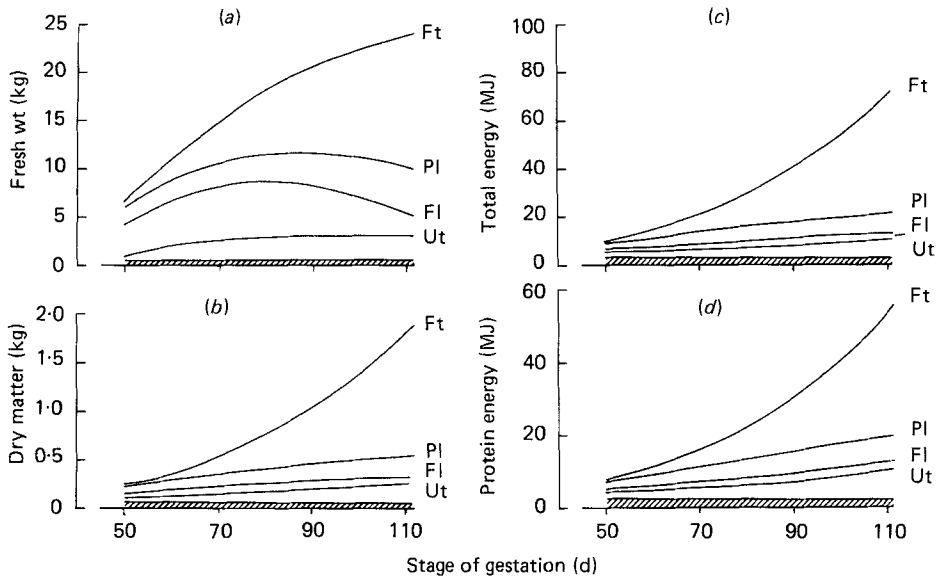

Fig. 1. Predictions of the growth and development of the gravid uterus and its component tissues in the pregnant gilt. Values have been calculated for a metabolizable energy (ME) intake of 30 MJ/d and for a litter size of twelve piglets. (*a*), Fresh weight; (*b*), dry matter; (*c*), total energy; (*d*), protein energy; Ft, fetus; Pl, placenta; Fl, fluids; Ut, empty uterus; (▨), non-pregnant uterus.

litter size (range nine to fourteen fetuses) and the lower gestational age of the animals at slaughter. The regression equations relating the weight of the individual uterine components to stage of gestation, level of energy intake and litter size are given in Table 3.

There were marked changes in the functional development of the individual uterine components. The contribution each made to the total weight of the gravid uterus is illustrated in (Fig. 1(*a*)). In early gestation the weight of fluids and placenta were greatest, contributing 66% of the total weight of the gravid uterus. Whereas the fluids attained maximal values in mid-gestation, the remaining tissues increased with stage of gestation. The weight of the fetal tissue was only 8% of the total in early pregnancy, but increased to 40% at day 90 and 59% at day 110.

Although the total weight of the gravid uterus increased with stage of gestation, maximum daily rates of gain occurred during mid-pregnancy (420 g/d at day 60) (Fig. 2(*a*)) when daily growths of the fluids were maximal. Following this, the relative growth rates of the fluids diminished to become negative by day 80. The rates of gain of both the placenta and empty uterus were small relative to those of the fetuses which increased from 66 g/d at day 50 to 290 g/d at day 110. The overall effect of these changes was a reduction in the relative growth rate of the gravid uterus from 367 g/d at day 50 to 193 and 160 g/d at days 90 and 110 respectively.

DM. In general, DM content increased with stage of gestation at each feeding level (Table 4). In early gestation there was little difference ($P > 0{\cdot}05$) in DM content between feeding levels, whereas in late gestation the values were higher at the higher feeding level. Calculations from the Gompertz equations presented in Table 4 show that total DM increased almost eight-fold between days 50 and 110 of gestation compared with only 3·7-fold for fresh weight. As a result, the DM content of the gravid uterus increased from 74·6 g/kg at day 50 to 103·1 and 159·0 g/kg at days 90 and 110 respectively. Although the empty uterus made the largest contribution to total DM in early gestation, the contribution of the fetal

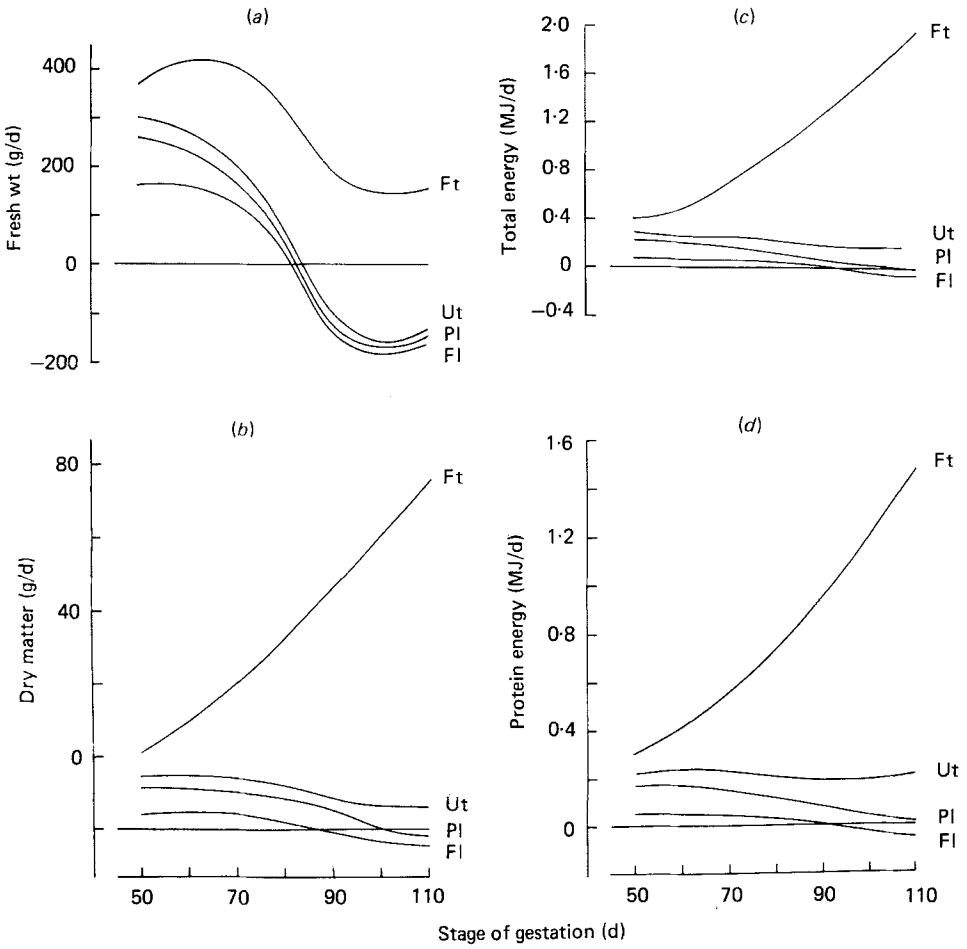

Fig. 2. Predictions of the growth rate of the gravid uterus and its component tissues in the pregnant gilt. Values have been calculated at a metabolizable energy intake of 30 MJ/d and for a litter size of twelve piglets. (*a*), Fresh weight; (*b*), dry matter; (*c*), total energy; (*d*), protein energy; Fe, fetus; Pl, placenta; Fl, fluids; Ut, empty uterus.

tissue increased from 0·12 at day 50 to 0·55 and 0·71 at days 90 and 110 respectively (Fig. 1(*b*)).

The variation in the daily rate of DM accretion in the uterine tissues is illustrated in Fig. 2(*b*). The increase in total DM with stage of gestation was primarily associated with the fetus. These changes are reflected in the proportion of DM contributing to the total rate of gain. At day 50 of gestation each 100 g increase in fresh weight was associated with only 4·9 g DM, whereas at days 90 and 110 this had increased to 33·7 and 94·0 g DM respectively.

Energy. The variation in the energy contents of the various uterine tissues was small; the highest coefficient of variation recorded was 3·5% (Table 5). There was no apparent trend in the extent to which the values for the individual tissues changed in relation to the stage of gestation; for example, the lowest values for the fetal and fluid tissues were determined in mid-gestation, but this pattern was not observed for the placenta and empty uterus. Level of feed intake did not influence the energy content of the uterine tissue. Over the stages

Table 4. *The dry matter content (g/kg) of the uterine tissues of pregnant gilts in relation to stage of gestation and level of energy intake*

(Mean values with their standard errors)

Stage of gestation (d)		Fetus		Placenta		Fluids		Empty uterus	
Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
				Low intake (20 MJ ME/d)					
51	1	103·9	2·7	65·3	4·5	12·2	2·5	128·1	1·2
79	1	118·4	0·9	81·0	1·7	16·0	2·2	129·0	2·5
102	3	150·1	6·8	80·8	5·8	13·4	2·5	144·0	3·0
				High intake (30 MJ ME/d)					
53	2	105·0	1·0	69·8	3·8	11·0	0·9	128·4	5·0
72	2	111·4	4·4	75·2	2·8	13·2	0·7	127·3	3·4
103	2	169·0	6·9	91·6	2·9	19·4	1·2	151·6	6·4

ME, metabolizable energy.

Regression equations relating the dry matter (DM; g) of the individual uterine tissues and total gravid uterus to stage of gestation (t; d), no. of fetuses (n) and level of energy intake (f; MJ ME/d):

Fetus: $\log_e DM = 7{\cdot}49993 - 5{\cdot}06045 \exp(-0{\cdot}02285(t-45)) + 0{\cdot}000253 ft + 0{\cdot}06097 n$ (R^2 0·99),

Placenta: $\log_e DM = 4{\cdot}43824 - 1{\cdot}15972 \exp(-0{\cdot}06074(t-45)) + 0{\cdot}000177 ft + 0{\cdot}08729 n$ (R^2 0·93),

Fluids: $\log_e DM = -1{\cdot}59820 + 0{\cdot}13067\, t - 0{\cdot}000744\, t^2 + 0{\cdot}09494\, n$ (R^2 0·89),

Empty uterus: $\log_e DM = 1{\cdot}93132 + 2{\cdot}47475 \exp(+0{\cdot}00348(t-45)) + 0{\cdot}000164 ft + 0{\cdot}06028 n$ (R^2 0·86),

Total gravid uterus: $\log_e DM = 8{\cdot}63031 - 3{\cdot}74855 \exp(-0{\cdot}01081(t-45)) + 0{\cdot}000191 ft + 0{\cdot}06892 n$ (R^2 0·98)

of gestation investigated, there was a seven-fold increase in the total energy contained in the pregnant uterus (Fig. 1(*c*)). In early pregnancy the energy content of the empty uterus represented approximately 50% of the total energy. However, the exponential growth of the fetuses resulted in fetal energy, as a percentage of the total, increasing from 12% at day 50 to 54 and 69% at days 90 and 110 respectively. Thus the energy content of the total gravid uterus changed with increase in stage of gestation, from 20·5 kJ/g DM at day 50 to 18·9 and 19·3 kJ/g DM at days 90 and 110 respectively.

The patterns of the rates of change of energy were similar to those of fresh weight and DM, with the fetal and empty uterine components increasing with stage of gestation whereas those of the placenta and fluids decreased (Fig. 2(*c*)). At day 110 the rate of fetal energy accretion represented 90% of the total.

N. In general, the N content of the tissues increased as pregnancy advanced, with the values in late pregnancy being higher at the higher level of feeding (Table 6). However, when the results were expressed on a DM basis there was no difference between the values at the different stages of gestation and feeding level, the mean (with SE) values were 0·090 (0·002), 0·101 (0·004), 0·098 (0·003) and 0·128 (0·002) g/g DM for fetal, placental, fluid and uterine tissue components respectively.

Assuming that the N content of protein is 0·16 g/g and that the energy value of protein is 23·8 kJ/g (Brouwer, 1965), the protein-energy content of the uterine tissues was calculated and subjected to a multiple-regression analysis (Table 6). The extent to which the various uterine tissues contributed to protein deposition is illustrated in Figs. 1(*d*) and 2(*d*) respectively. These show that the patterns of change were similar to those for energy. As a percentage of the total energy retention, protein energy varied within the narrow range 77–81%. In early pregnancy the major contributor to protein retention was the uterus, while

Table 5. *The energy content (kJ/g DM) of the uterine tissues of pregnant gilts in relation to stage of gestation and level of energy intake*

(Mean values with their standard errors)

Stage of gestation (d)		Fetus		Placenta		Fluids		Empty uterus	
Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
				Low intake (20 MJ ME/d)					
51	1	19·69	0·14	19·62	0·30	18·27	0·19	21·77	0·13
79	1	18·03	0·14	19·73	0·45	16·53	0·22	20·91	0·07
102	3	19·21	0·24	20·64	0·34	17·22	0·61	21·73	0·18
				High intake (30 MJ ME/d)					
53	2	19·40	0·13	20·11	0·21	17·66	0·29	21·69	0·85
72	2	18·32	0·24	20·64	0·31	16·69	0·40	21·26	0·42
103	2	18·55	0·43	20·00	0·29	17·92	0·34	20·05	0·47

ME, metabolizable energy; DM, dry matter.

Regression equations relating the energy content (E; kJ) of the individual uterine tissues and total gravid uterus to stage of gestation (t; d), no. of fetuses (n) and level of energy intake (f; MJ ME/d):

Fetus: $\log_e E = 10{\cdot}77958 - 5{\cdot}29435 \exp(-0{\cdot}02015\,(t-45)) + 0{\cdot}000228 ft + 0{\cdot}06086\, n$ (R^2 0·99),

Placenta: $\log_e E = 7{\cdot}36942 - 1{\cdot}18834 \exp(-0{\cdot}06812\,(t-45)) + 0{\cdot}000187 ft + 0{\cdot}08959\, n$ (R^2 0·95),

Fluids: $\log_e E = 2{\cdot}12564 + 0{\cdot}11013\, t - 0{\cdot}000613\, t^2 + 0{\cdot}08418\, n$ (R^2 0·86),

Empty uterus: $\log_e E = 6{\cdot}97531 + 0{\cdot}64081 \exp(+0{\cdot}01063\,(t-45)) + 0{\cdot}000122 ft + 0{\cdot}05508\, n$ (R^2 0·87),

Total gravid uterus: $\log_e E = 12{\cdot}95297 - 4{\cdot}97615 \exp(-0{\cdot}00704\,(t-45)) + 0{\cdot}000182 ft + 0{\cdot}06611\, n$ (R^2 0·98).

Table 6. *The nitrogen content (g/kg fresh weight) of the uterine tissues of pregnant gilts in relation to stage of gestation and level of energy intake*

(Mean values with their standard errors)

Stage of gestation (d)		Fetus		Placenta		Fluids		Empty uterus	
Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
				Low intake (20 MJ ME/d)					
51	1	9·5	0·2	5·7	0·6	1·3	0·2	15·7	0·7
79	1	10·2	0·7	8·5	0·3	1·5	0·2	16·6	1·0
102	3	13·2	0·3	8·8	0·9	1·2	0·2	18·1	0·3
				High intake (30 MJ ME/d)					
53	2	10·2	0·1	6·3	0·9	1·2	0·2	17·7	0·8
72	2	9·7	0·2	7·9	0·6	1·2	0·1	15·9	0·6
103	2	15·4	0·7	10·2	0·7	2·0	0·2	19·6	1·0

ME, metabolizable energy.

Regression equations relating the protein-energy content (P; kJ) of the individual uterine tissues and total gravid uterus to stage of gestation (t; d), no. of fetuses (n) and level of energy intake (f; MJ ME/d):

Fetus: $\log_e P = 10{\cdot}06598 - 5{\cdot}03236 \exp(-0{\cdot}02116\,(t-45)) + 0{\cdot}000299 ft + 0{\cdot}06397\, n$ (R^2 0·99),

Placenta: $\log_e P = 7{\cdot}34264 - 1{\cdot}40598 \exp(-0{\cdot}06250\,(t-45)) + 0{\cdot}000253 ft + 0{\cdot}06339\, n$ (R^2 0·94),

Fluids: $\log_e P = 2{\cdot}39536 + 0{\cdot}09807\, t - 0{\cdot}000541\, t^2 + 0{\cdot}08734\, n$ (R^2 0·84),

Empty uterus: $\log_e P = 7{\cdot}02748 + 0{\cdot}33484 \exp(+0{\cdot}01489\,(t-45)) + 0{\cdot}000203 ft + 0{\cdot}05826\, n$ (R^2 0·85),

Total gravid uterus: $\log_e P = 12{\cdot}21245 - 4{\cdot}46636 \exp(-0{\cdot}00722\,(t-45)) + 0{\cdot}000230 ft + 0{\cdot}06217\, n$ (R^2 0·98).

Table 7. *The chemical composition of the mammary tissue of pregnant gilts in relation to stage of gestation and level of energy intake*

(Mean values with their standard errors)

Stage of gestation (d)		Wt (g)		Dry matter (DM; g/kg)		Energy (kJ/kg DM)		Nitrogen (g/kg fresh weight)	
Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
				Low intake (20 MJ ME/d)					
79	1	902	59	579·6	50·9	36·16	1·55	10·9	1·8
102	3	1347	265	416·8	39·7	34·12	0·57	17·3	1·5
				High intake (30 MJ ME/d)					
72	2	904	157	619·4	20·9	37·10	0·31	8·5	0·2
103	2	2885	293	479·5	31·5	34·37	0·54	16·5	1·5

ME, metabolizable energy.

Regression equations relating the fresh weight (W; g), dry matter (DM; g), total energy content (E; kJ) and the energy retained as protein (P; kJ) in mammary tissue to stage of gestation (t; d) and level of energy intake (f; MJ ME/d):

Fresh wt: $\log_e W = 5{\cdot}16091 + 0{\cdot}07997 \exp(+0{\cdot}04576\ (t-45)) + 0{\cdot}05225 f$ (R^2 0·79),

Dry matter: $\log_e DM = -4{\cdot}83042 + 8{\cdot}98959 \exp(+0{\cdot}00173\ (t-45)) + 0{\cdot}06542 f$ (R^2 0·59),

Total energy: $\log_e E = 0{\cdot}92380 + 6{\cdot}89773 \exp(+0{\cdot}00185\ (t-45)) + 0{\cdot}06654 f$ (R^2 0·54),

Protein energy: $\log_e P = 1{\cdot}43401 + 3{\cdot}32153 \exp(+0{\cdot}00991\ (t-45)) + 0{\cdot}04803 f$ (R^2 0·84).

in late pregnancy it was the fetus. The overall effect of the change in the growth and protein content of the tissues was a decrease in the protein-energy content of the total gravid uterus from 16·6 kJ/g DM at day 50 to 14·9 kJ/g DM at day 110 of gestation.

Mammary tissue

As indicated by the large standard errors, the fresh weight of the mammary tissue was extremely variable, particularly in late gestation (Table 7). For example, at the high feed intake the weight of the mammary tissue in late gestation varied between 1843 and 4056 g. Both stage of gestation and level of feed intake had a significant effect on the weight of mammary tissue ($P < 0{\cdot}05$). At both levels of feeding there was a significant decrease in DM content as stage of gestation increased ($P < 0{\cdot}05$). Energy content also decreased with stage of gestation, although the differences were not significant ($P > 0{\cdot}05$). In comparison, N retention increased with duration of pregnancy, with the effect being independent of feeding level. The percentage of fat, calculated as the difference between total energy and the energy retained as protein, decreased over the periods of pregnancy investigated, from 52% in mid-pregnancy to 32% in late pregnancy.

Although the chemical composition of the mammary tissue appeared quite similar at each stage of gestation and feeding level, there were large variations in fresh weight and this influenced the choice of model used for the calculation of total composition. Examination of the results revealed that the weight and chemical composition of the mammary tissue increased exponentially with stage of gestation, with level of feeding having an additional significant influence. The effect of litter size was not significant ($P > 0{\cdot}05$). The resulting relations are presented in Table 7.

DISCUSSION

The use of the modelling procedures

The primary purpose of this investigation was to measure the rate of nutrient deposition in the uterus of the pregnant gilt throughout gestation. In this respect, and in agreement with the investigations of Laird *et al.* (1965), Laird (1966) and Robinson *et al.* (1977), the Gompertz equation fitted the results well and hence gave a close representation of the pattern of tissue accretion involved in the growth and development of the gravid uterus. These investigations have shown that the exponential decline in specific growth rate was a feature of intra-uterine development and that the Gompertz equation allowed this to be described mathematically. The model of Koong *et al.* (1975), in which a quadratic function of time replaces the exponential, was used only for mammary tissue, since the exponential dependence on time was more reliable for prediction of absolute values and particularly rates of change at the limits of the data. In addition, Koong *et al.* (1975) found that the level of nutrition did not have a significant effect on the growth of lambs *in utero* and excluded it from their model. In the present experiments, feed intake had a significant effect, thus necessitating its inclusion. Similarly, litter size was also included.

The Gompertz formulation fulfilled the basic criteria that the selected model should have the highest degree of correlation and the smallest residual sums of squares. The difference between the values for the total gravid uterus derived from the model and from the sum of the individually-predicted uterine tissues was less than 2%. The model has been used to make predictions only between days 45 and 110 of gestation since this is the range of gestational ages examined in the present experiments. It is during this period that the most significant changes in the growth and development of the gravid uterus and mammary tissue occur and in which information is required for specifying how the changes in these tissues influence the maternal nutrient requirements.

Deposition of reproductive tissue

The results in Figs. 1 and 2 show the differences in functional development of the various uterine tissues and the degree to which they contribute to total uterine development. Like the results of Mitchell *et al.* (1931), Pomeroy (1960) and Moustgaard (1962), they show a ten-fold increase in the fresh weight of the gravid uterus and its DM, energy and protein contents. There are, however, differences in the pattern of growth, and development depending upon the constituent analysed. In early gestation, for example, it was the weight of the fetal fluids which had the most marked effect on uterine growth, and during this period the DM content of the gravid uterus was lowest, approximately 70 g/kg. As gestation proceeded, the growth and chemical contents of the fluid, placental and empty uterine components were reduced relative to those of the fetuses so that at parturition the fetal gain represented between 60 and 70% of the total gravid uterus. This resulted in the DM content of the gravid uterus increasing to 160 g/kg at day 110. However, there was no progressive variation in the energy and N contents of the gravid uterus when expressed on a DM basis, with respective values of 19·5 kJ/g DM and 0·099 g N/g DM from mid-pregnancy onwards.

There have been few extensive studies on nutrient deposition in the gravid uterus which allow direct comparison with the present results. Mitchell *et al.* (1931) concluded from their studies that a pregnant gilt carrying an average litter of eight piglets would be expected to deposit 1138 kJ energy and 33 g crude protein/d at the termination of pregnancy. This may be compared with daily rates of energy and protein deposition of 1516 kJ and 50 g at day 110 of gestation in the present study. For a litter of ten piglets, it may be calculated from the results of Moustgaard (1962) that the pregnant gilt would have an energy and protein deposition of 1838 kJ/d and 57 g/d respectively at day 110 of gestation. The corresponding

Table 8. *The predicted rates of energy (kJ/d) and protein (g/d) accretion in the reproductive tissue of pregnant gilts, partitioned into gravid uterine and mammary tissue components*

(The values have been calculated for a litter size of twelve piglets and at metabolizable energy (ME) intakes of 20 and 30 MJ/d)

Stage of gestation (d)	Gravid uterus		Mammary tissue		Total	
	Energy	Protein	Energy	Protein	Energy	Protein
			Low intake (20 MJ ME/d)			
50	349	11	141	1	490	12
70	624	19	190	2	814	21
90	1030	32	259	4	1289	36
100	1289	39	304	8	1593	47
110	1586	48	357	17	1943	65
			High intake (30 MJ ME/d)			
50	391	13	244	1	635	14
70	724	24	330	2	1054	26
90	1238	40	449	7	1687	47
100	1577	51	526	13	2103	64
110	1976	64	619	25	2595	89

values from the present results are 1731 kJ/d and 57 g/d. From this it may be concluded that under conditions of adequate maternal nutrition, the rate of nutrient assimilation in the gravid uterus is relatively insensitive to external influences.

Although it is necessary to describe the gross changes in reproductive tissue, that is both gravid uterus and mammary tissue, it is the specific rates of gain which are important, since any change in the rate of tissue accretion represents a change in the requirements for nutrients. For this purpose Table 8 has been constructed to show the rate of energy and protein accretion in the reproductive tissues during gestation. If it is assumed that energy is accreted with an efficiency of 0·80 (Agricultural Research Council, 1981), it may be calculated that as pregnancy progresses from day 50 to day 110, the ME requirement for reproductive gain increases from 0·03 to 0·12 of maternal energy intake. The corresponding values for protein have been calculated on the basis that the digestibility of protein is 0·74 (Close *et al.* 1985) and that the efficiency with which protein is utilized is 0·70 (Ferrell *et al.* 1976; Agricultural Research Council, 1981). The calculated requirement for protein as a proportion of intake is greater than that of energy, increasing from 0·07 of maternal digestible protein intake at day 50 of gestation of 0·41 at day 110. In terms of protein deposition, the growth and development of the reproductive tissue therefore make considerable demands on maternal feed supply, especially in late gestation. These values for energy and protein only represent rates of accretion and do not take into account the requirement for the maintenance of the reproductive tissue. However the computations show the usefulness of the equations presented in Tables 3–7 in calculating the nutrient requirements for reproductive gain.

Fetal weight

In practice it is important to identify those factors which influence fetal weight since the greater the body-weight the greater the piglet's energy reserves at birth and chances of survival. The present results, in common with other studies (McKeown *et al.* 1976), show an indirect relation between litter size and fetal weight but a direct relation between plane of nutrition and fetal weight, with the effect of the latter being most pronounced in late gestation. Since the fetus is dependent on the mother for its nutrient supply, it is not surprising

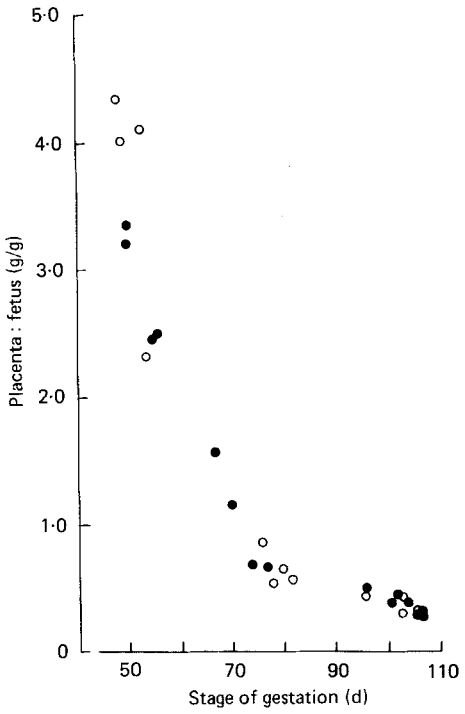

Fig. 3. The relation between the weight of the placenta and the weight of the fetus in the pregnant gilt. (○), 20 MJ metabolizable energy (ME)/d; (●), 30 MJ ME/d.

that its weight varies with the nutritional status of the mother. However, the 16% reduction in fetal weight at term on the low feed intake compared with that on the high feed intake was greater than anticipated. Factors responsible for this reduction appear to be concentrated in late gestation since, before day 80, maternal feed intake appeared to have little influence on fetal weight (Table 3).

The variations in fetal weight in late gestation are highly correlated with variations in placental weight associated with changes in both litter size and level of feed intake, so that the heavier the fetus the greater the placental weight. However, when expressed relative to the weight of the fetus, placental weight was independent of feed intake at any period of pregnancy investigated (Fig. 3). McLaren (1965) has postulated that it is the size of the placenta *per se* which influences nutrient transfer to the fetus and hence fetal growth. The rate of fetal tissue accretion may therefore be indirectly influenced by maternal nutrient supply, the primary influence being on the growth of the placenta. On the basis that placental size is concomitant with placental efficiency, and since differences only become apparent in late gestation, it may be hypothesized that placental and hence fetal growth is independent of maternal nutrient intake at least up to day 80 of gestation (Table 3). When energy is limited in early gestation the cellular growth of the placenta is limited and hence may be unable to respond to nutritional rehabilitation, although the effect appears to be apparent only in late gestation. This may explain why attempts to improve the energy status of the new-born piglet by maternal dietary supplementation in late gestation have failed to produce any appreciable change in its carbohydrate or fat content (Moser & Lewis, 1980; Pettigrew, 1981; Seerley, 1981).

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Printed in Great Britain