THE ENERGY AND NITROGEN METABOLISM AND PERFORMANCE OF PIGS INFECTED WITH *OESOPHAGOSTOMUM DENTATUM*

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ABSTRACT

Two experiments, in which energy and protein metabolism and growth were measured, investigated the effects of infection with the nodular worm Oesophagostomum dentatum on growing pigs.

In the first experiment, eight gilts were randomly assigned to one of two infection treatments (infected or uninfected). Each infection treatment was then randomly assigned to one of two planes of nutrition (high-plane or low-plane). Those being infected were dosed orally at 20 kg liveweight with 80,000 O.dentatum third stage larvae. Energy and nitrogen balances were repeated serially three times on each animal. Two open-circuit calorimeters were used, with the different treatments being distributed equally to each of these.

O.dentatum eggs appeared in the faeces 19-26 days after administration of the larval dose, increased to a maximum concentration ranging between 4,475 and 18,275 eggs per gram (epg) faeces after 7 weeks and fell to concentrations ranging between 250 and 11,775 epg faeces at slaughter. All uninfected animals remained worm-free.

Heat production (HP) and metabolizable energy intake (ME) were proportional to liveweight$^{0.66}$ ($LW^{0.66}$). Therefore $LW^{0.66}$ was used as the base to reduce variability in the data caused by variation in liveweight (LW).

There were no significant differences between infected and uninfected pigs for intake, digestibility, metabolizability or retention of energy and nitrogen.

Regression analyses of ER vs ME allowed ME required for maintenance (ME_m) and the efficiency of utilization of ME for growth (k_g) to be

calculated. The pooled value for ME_m was 0.69 $MJ.kg^{-0.66}.day^{-1}$ or 0.49 $MJ.kg^{-0.75}.day^{-1}$.

The pooled value for k_g was 0.54 (calculated on the basis of $MJ.kg^{-0.66}.day^{-1}$) or 0.56 (caluclated on the basis of $MJ.kg^{-0.75}.day^{-1}$). There were no significant differences between treatments for either ME_m or k_g.

In the second experiment, twenty-eight boars and gilts were assigned to one of two infection treatments (infected or uninfected). Those being infected were dosed at 20 kg liveweight with 80,000 O.dentatum third stage larvae. All pigs were individually fed once daily on the same feeding scale. They were weighed weekly and slaughtered at approximately 80 kg liveweight and the digestive tracts recovered.

O.dentatum eggs appeared in the faeces at approximately 3 weeks post-infection, rose to a maximum concentration ranging between 2,825 and 36,250 (average 19,907) epg faeces at 6-13 weeks and then declined to between 50 and 25,825 (average 11,060) epg fresh faeces at slaughter. All uninfected animals remained egg-free.

Average worm numbers recovered after slaughter were 4,255 per pig from infected animals. No worms were recovered from uninfected pigs.

No differences were found between infected and uninfected pigs for growth or carcass characteristics.

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CHAPTER ONE

LITERATURE REVIEW

Energy Metabolism and Nutrition of the Growing Pig

1.1 A System for Describing the Energy Requirements of Pigs: The Metabolizable Energy System

The practical objective of any energy system is to make it possible to firstly, predict the performances of animals from an understanding of the foods, secondly, to formulate rations to support a given level of performance and thirdly, to enable the relative values of feedstuffs for a given purpose to be accurately assessed. A satisfactory system must take into account:

1. The large variety of ingredients available
2. The effect of various combinations of these ingredients together with the level of feeding
3. Variations in the environment
4. Differences in the productive capacities of the animals.

The Metabolizable Energy (M.E.) system, which has recently had considerable support in both pig and poultry nutrition and which has now been adopted by the ARC for cattle, is a distinct improvement on Starch Equivalent (S.E.) or Total Digestible Nitrogen (TDN) in that it allows the different efficiencies with which energy is used for the various aspects of production (e.g., growth, lactation, pregnancy) to be accounted for (Filmer and Curran, 1977).

In calculating M.E., the amount of energy lost in the urine is deducted from the Digestible Energy (D.E.). It is important to take the protein relationships into account and to calculate the M.E. of the diet from a knowledge of the D.E. intake and the protein deaminated. M.E. values of raw materials are thus not strictly additive (factorial) when foods are combined into a diet because urinary losses vary with nutrient balance, level of feeding and the stage of growth and genetic potential of the pig (Crampton et al., 1957).

Morgan et al. (1975a; 1975b) determined D.E. and M.E. for a range of feedstuffs. They concluded that adoption of a nitrogen-corrected M.E. system was preferable to the use of D.E. for all classes of livestock.

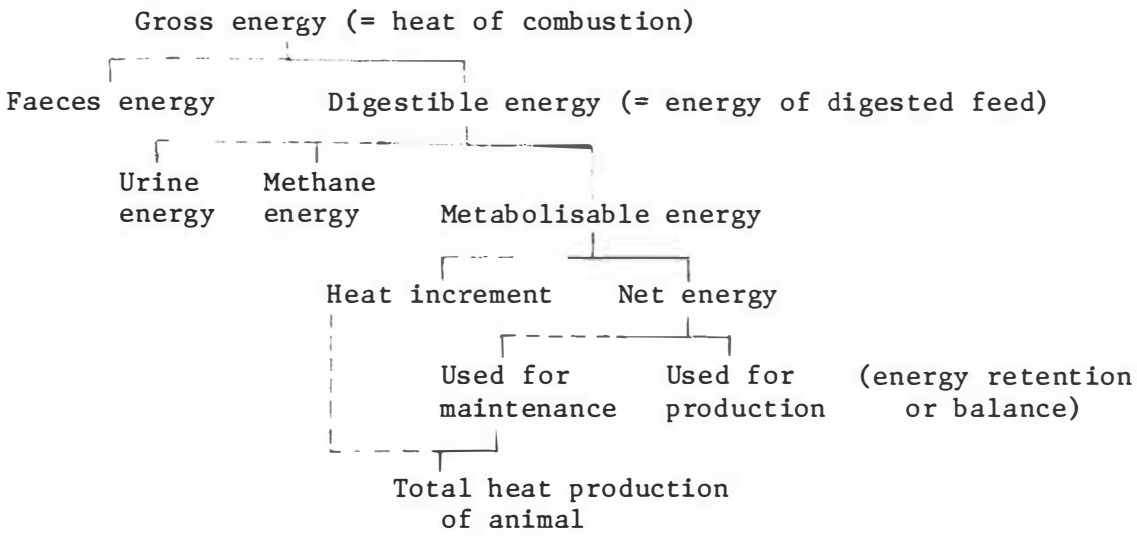
1.2 The Partition of Food Energy

The growing pig requires the energy-yielding components of its diet for many purposes. Under normal circumstances the proteins, lipids and fats which are digested and absorbed are used as the primary units of a wide range of metabolic processes. Expressing the Gross Energy (G.E.) released on combustion in kilojoules per gram gives the maximal energy value for any dietary constituent but this is not a satisfactory means for describing the nutritive value of diets used in practice (see Fig. 1.1). The major discrepancy between G.E. and the energy which is useful to the pig is the energy which is lost in faeces (F.E.). Not all F.E. is feed residue, since endogenous secretions such as digestive juices are not perfectly reabsorbed. For this reason, (G.E. - F.E.) is often referred to as apparently digested energy, since true digestibility implies a correction for material of endogenous origins. Apparently digested energy (D.E.) can be determined relatively simply by digestibility trials and comprehensive tables giving values

of D.E. for a wide range of feed constituents are available, e.g., McDonald et al. (1973), N.R.C. (1968), ARC (1967). There is a continuing debate as to whether or not additional refinements of D.E. are useful in formulating foods for pigs (Fowler, 1978). Values of D.E. take no account of urinary losses of energy arising from digested protein which is subsequently deaminated and of the nitrogenous fraction used in the synthesis of urea. A fraction of the digested dietary energy not available to the animal is contained both in the urine and in the combustible gases which arise from bacterial fermentation in the hindgut. Subtraction of these losses from D.E. gives Metabolizable Energy (M.E.). The concept of M.E. describes the partition of M.E., the energy which is available for partition among different metabolic processes. For the pig, the collection of urine quantitatively and the determination of its energy value is not difficult. M.E. provides a more accurate estimate of the energy available to the pig compared with D.E. The description of dietary M.E. can be refined and described in terms of nitrogen-corrected M.E., in which adjustments are made to correct the value to either zero nitrogen retention, or to some fixed positive nitrogen retention bases on a given fraction of the protein supplied (Fowler, 1978).

The ingestion of food by an animal is followed by losses of chemical energy (above), and also by loss of heat. This heat loss is known as the Heat Increment (H.I.), and its cause lies mainly with the energetic inefficiency of the reactions by which absorbed nutrients are metabolized. A further part of the heat increment is attributable to the process of digestion, in mastication of food and its propulsion through the alimentary tract. Chemical energy used for this work is converted into heat. The deduction of the Heat Increment of a food

Fig. 1.1 The Partition of Food Energy in the Animal (From McDonald et al, 1973).



from its M.E. gives the Net Energy (N.E.) value of the food. This N.E. is that energy which is available to the animal for useful purposes, i.e. for body maintenance and for the various forms of production. Heat resulting from maintenance represents the end-product of useful energy which has been degraded through use to another (useless) form of energy. Of the heat loss from the animal, only the heat increment of the food is waste (McDonald et al, 1973).

As ME_I rises from zero to maintenance level (distance AC, Fig.1.2), heat production rises by distance BC. At maintenance the apparent heat increment is therefore 100 $^{BC}/_{AC}$. Basal Metabolism (Fasting Heat Production, F.H.P.) is the term which describes heat production in the postabsorptive fasting, resting, thermoneutral animal. In the fasting animal a proportion of the total heat production arises during the transference of energy from body fat to ATP, (distance AE), which represents the heat increment of body fat. As food intake increases to the level needed for maintenance, the heat arising from the metabolism of body fat decreases, (triangle ADE) and that arising from the utilization of food constituents increases, (triangle ABD). The proportion 100 x $^{BD}/_{AC}$ therefore provides a more accurate estimate of the efficiency with which M.E. is used for maintenance, and this would be the so-called "true" k_m. In Fig. 1.2, the line DE is known as the minimum base value of heat production, which is a theoretical value, and which cannot be measured. Above maintenance the heat increment is given by the expression 100 $^{FG}/_{BG}$ (McDonald et al, 1973).

1.3 The Use of Dietary Energy

Estimations of the requirement of M.E. for maintenance, growth, protein and fat formation have been obtained by different methods for different species, as discussed in detail by Blaxter (1972) and Van Es (1972). It is conventional to express this requirement in relation to metabolic liveweight, $kg^{0.75}$ (see Klieber, 1965, and later section 1.4.2), but some uncertainty still exists concerning the most valid exponent of liveweight (Thorbek and Henckel, 1976).

The fact that N.E. is a precise measure which can be duplicated

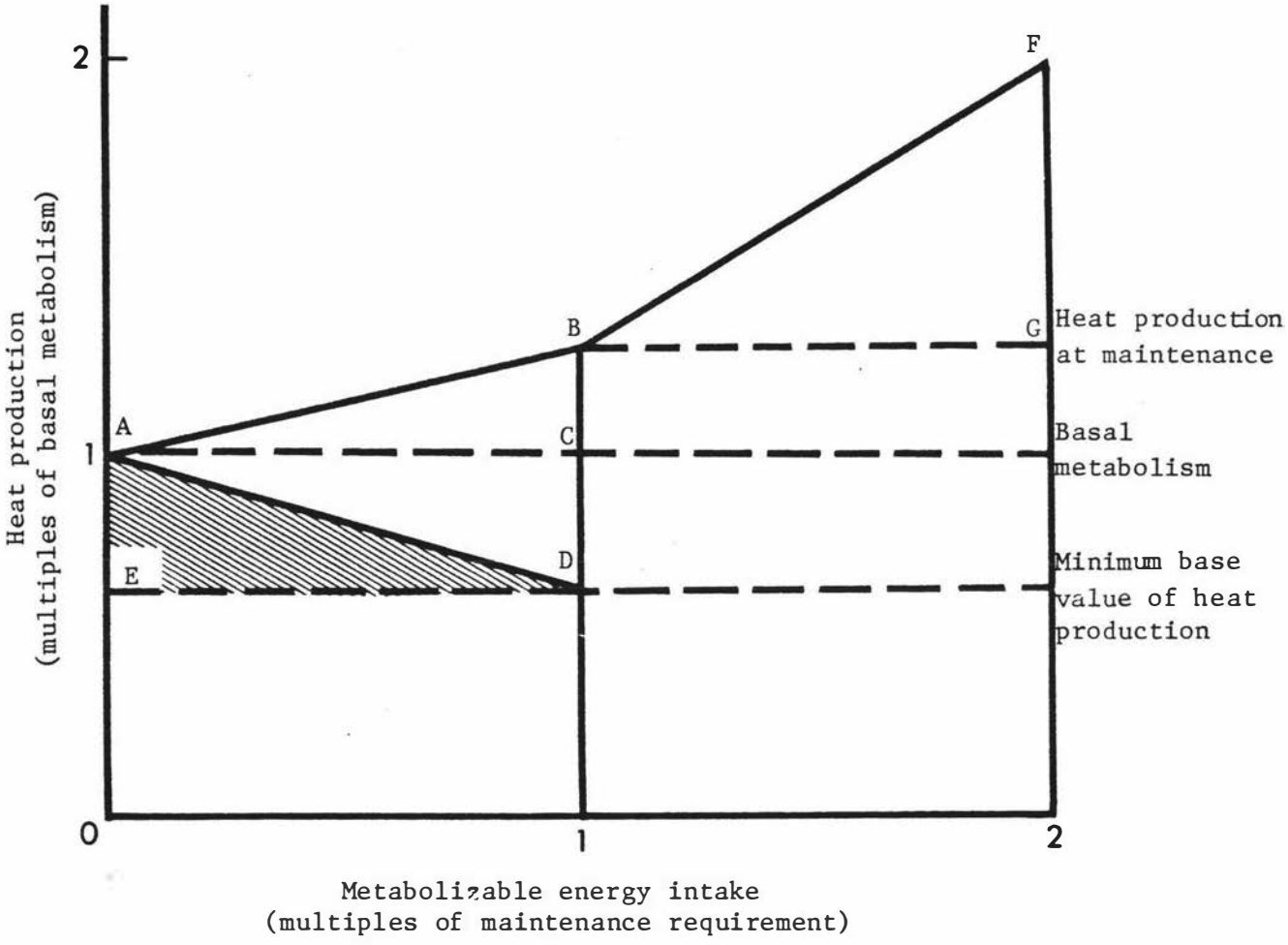


Figure 1.2 Relationship between heat production and metabolizable energy intake (From McDonald et al, 1973).

Total heat production is represented by line ABF.

only under specific conditions should not lead to the conclusion that D.E. or M.E. is to be preferred simply because repeatable determinations are more easily obtained. Repeatability is not to be confused with precision. The same factors which operate to influence a N.E. value also ultimately influence the utilization of D.E. and M.E. (Meyer and Garrett, 1967). The efficiency with which dietary energy is converted to animal product is dependant on five main factors (Webster, 1974):

1. That portion of G.E. serving as a fuel for body functions, called M.E. The gross efficiency of retention of M.E. is:

$$(ME_I - H)/ME_I = \frac{ER}{ME}$$

where ME_I = intake of metabolizable energy

H = metabolic heat production

2. The requirement for mainteance ($M.E._m$) of vital body functions, conventionally taken as the intake of M.E., (ME_I) which results in M.E. being equal to metabolic heat production (H). H is the sum of fasting metabolism, the energy cost of activity and the heat increment of feeding.

3. The net efficiencies with which increments of M.E. are used above and below maintenance (Blaxter et al, 1972; Moe et al, 1969). These partial efficiencies vary not only because of differences in the chemical makeup of the feedstuff, but also because at least six separate and major metabolic functions may be occurring simultaneously and be interrelated. Enough information is available to suggest that maintenance, growth, fattening and lactation occur with different levels of partial efficiency (Blaxter, 1962; Reid, 1962; Brody, 1945); it is not unlikely that muscular activity and reproduction (Graham, 1964) function at yet different levels.

4. The partition of retained energy principally between protein

(ER_p) and fat (ER_f), which determines not only the chemical composition of the carcass but also the amount of energy stored per kg of carcass gain, influences gross efficiency of conversion of M.E. into body mass. The energy content of the dry matter of muscle protein is 23.5 kJ/g; each gram is associated with about five times its weight of water. Thus the energy content of 'wet'muscle protein is about 4.7 kJ/g. Lipid has an energy content of about 39.2 kJ/g so that the energy retained in a gram of fat is theoretically eight times greater than that retained in a gram of 'wet' protein. In practice the energy content of carcass gains ranges from about 8 kJ/g in a very young animal growing slowly to about 32 kJ/g in animals rapidly approaching slaughter-weight (90 kg) - a four-fold range (A.R.C., 1965). The relationship between energy retention (MJ) and weight (kg) of body tissue deposited can only be established if the composition of body gains are known very precisely. Thus, any attempt to predict the efficiency of M.E. utilization from body weight gains (or vice versa) without reliable measurements of body composition is meaningless.

5. The physiological limit to the capacity of the animal to consume food and store it. The gross efficiency of retention of M.E. ($^{ER}/_{ME_I}$) is principally a function of the amount by which ME_I exceeds maintentance, i.e., appetite. Pullar and Webster (1974) found that results with fat and lean Zucker rats suggested that both groups regulated their intake during growth to sustain the same rate of protein deposition or heat production, a finding subsequently confirmed by Radcliffe et al., (1975).

Heat production expressed per $kg^{0.75}$ is remarkably constant for a wide range of animals fed to appetite on a wide range of diets, at 780-807 kJ per $kg^{0.75}$ per 24 hours, although E.R. varies, according to the quality of the diet from 104 to 673 kJ per kg per 24 hours (Webster,

1974). From these results, Webster proposed that in animals given free access to a balanced diet, protein deposition and heat production appear to have rigidly defined upper limits which are set by the capacity of the animal for synthesis of lean body mass.

The pig normally controls its energy balance by adjusting its voluntary feed intake (Fowler, 1978). Several workers have shown that the pig will compensate for changes in the nutrient density of the diet by increasing or decreasing intake (Cole et al, 1967; Cole et al,1968; Cole et al, 1972; Owen and Ridgman, 1967; 1968). Within wide limits, the compensation tends to result in isocaloric intakes (Pullar and Webster, 1977). This suggests an inherent appetite for digestible energy and the implications of this in programmes of pig breeding have been discussed by Fowler et al, (1976). Selection for efficient production of lean tissue in a selection environment which allows some but not complete expression of appetite may result in a rejection of pigs with inherently high intakes but which have an exceptional potential to deposit lean (Fowler, 1978).

Voluntary intake varies considerably both between pigs and from day to day in individuals. Houseman et al, (1978) noted variation of up to 25% in the weekly intake of individual pigs growing from 20 to 120 kg liveweight.

Intake is often considered to be a function of metabolic liveweight and feeding scales are frequently expressed in these terms. However, daily intake tends to reach an asymtote at a liveweight of 120-140 kg, and may then fluctuate markedly. Above 120 kg, very few data are available.

The equation $D.E. = 4.7W^{0.51}$ (Houseman *et al*, 1978) fitted their data adequately over the weight range to 20 to 120 kg liveweight.

Where D.E. = intake of digestible energy/day (MJ)

W = liveweight (kg).

The closeness of this to a simple square root function is of some interest, since relatively simple arithmetic allows calculation of voluntary feed intake at particular liveweights. The data of Houseman *et al*, (1978) can also be expressed as 141g/day of feed per $kg^{0.75}$ (metabolic liveweight) (Fowler, 1978).

1.4 Energy Requirements for Maintenance

The quantity of energy required for maintenance is by definition, that which promotes energy equilibrium, i.e. zero energy balance (Van Es, 1972). The ratio of M.E. sufficient to keep the animal at energy equilibrium to the animal's F.H.P. has been regarded as the energy efficiency for maintenance (k_m). This, however, should be called "apparent" efficiency, because the "true" energy expenditure for maintenance is certainly much lower than F.H.P. (Van Es, 1972, see page 2 for discussion).

During fasting, fat stored in the organism is catabolized to produce high-energy bonds, and these can be considered a source of energy for maintenance work. True M.E. for maintenance is probably $\sim$ 60% F.H.P.

Some estimates of the efficiency with which the energy of food nutrients are used by different species are presented by Blaxter

(1971), quoting results from several sources. The theoretical assumption that heat increment of nutrients used to meet maintenance requirements is inversely proportional to their deduced efficiency for ATP formation has been supported convincingly by the results of careful experiments with sheep (Armstrong, 1969). There are no experimental methods permitting the separation of the heat evolved by an animal into a portion resulting from the true work of maintenance and another portion connected with the formation of high-energy bonds (Kielanowski, 1972a).

1.4.1 Methods of estimating $M.E._m$ requirements

1. Fasting trials

$M.E._m$ may be calculated from F.H.P. if k_m is measured or assumed (see Fig. 1.3). Mature, non-producing animals are usually chosen. Their heat production or loss is measured near the end of a duration of fasting, either by direct or indirect calorimetry. Urine, through which energy losses occur, may also be measured so that the energy balance during fasting may be computed (Van Es, 1972). A fasted animal must oxidise reserves of nutrients to provide the energy for essential processes. Since the energy so utilized leaves the body as heat, the animal is then in a state of negative energy balance. The same holds true for other nutrients: an animal fed on a protein-free diet continues to lose N in its faeces and urine, and is therefore in negative N balance. The purpose of a maintenance ration is to prevent this drain on the body tissue (McDonald et al, 1973).

This standardized method cannot be used for lactating and for very young animals, because systematic errors made during fasting such

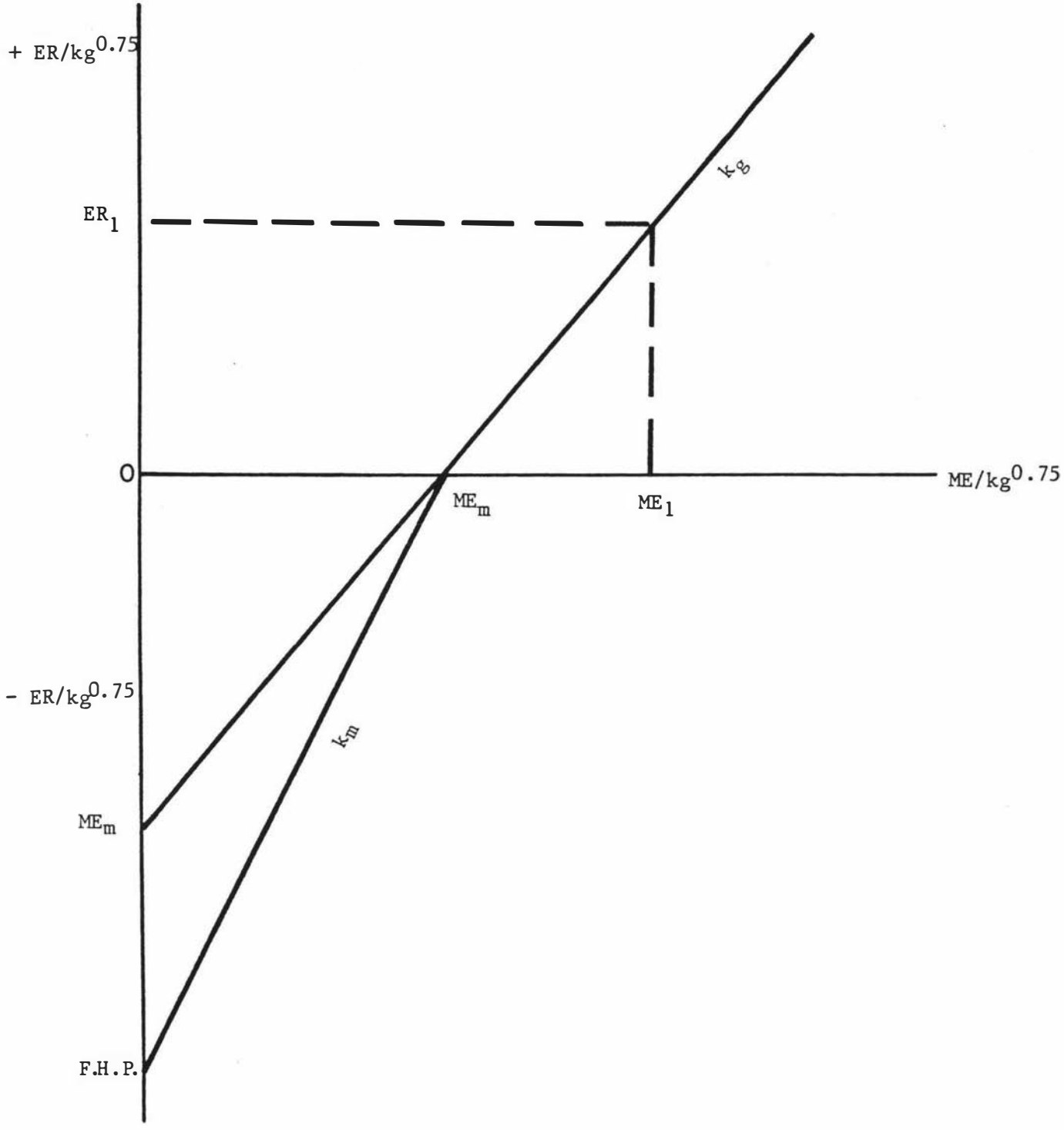


Figure 1.3 Utilization of ME by the animal.

Changes in ER which take place in response to changes in ME can be described as in Fig. 1.3

Figure 1.3

Since $\frac{FHP}{ME_m} = k_m$ (slope), if FHP and k_m are known,

ME_m can be caluculated.

Also, ME and ER can be measured, and ME_m when ER = 0 determined by interpolation. This is the basis of the F.H.P. and Feeding Methods calculations.

$$\frac{ER_1 - 0}{ME_1 - ME_m} = k_g \qquad \frac{ER_2 - ER_1}{ME_2 - ME_1} = k_g$$

Efficiency of use of M.E. for different metabolic function is denoted by:

k_m = efficiency of utilization of M.E. for maintenance

k_g = " " " " growth

k_f = " " " " fattening

k_p = " " " " protein

k_l = " " " " lactation

k_r = " " " " reproduction

(McDonald et al, 1973).

animals cannot be corrected by using appropriate values of maintenance efficiencies; neither are periods of feeding at the maintenance level (necessary for determining these values) really possible for such animals (Van Es, 1972).

Even from the results of excellent determinations of fasting energy balance, it is impossible, unless some assumptions or further measurements are made, to derive an accurate figure for ME_m of the animal when fed, ie., the "apparent" efficiency of the utilization of M.E. for maintenance is not comparable with a similar figure derived for fat production by feeding quantities of M.E. of the same ration at and above the maintenance feeding level. The "apparent" maintenance efficiency figure is of a far more complicated character than the (true) fattening efficiency figure. The former may be measured fairly easily; the latter can only be estimated indirectly (Armstrong, 1968).

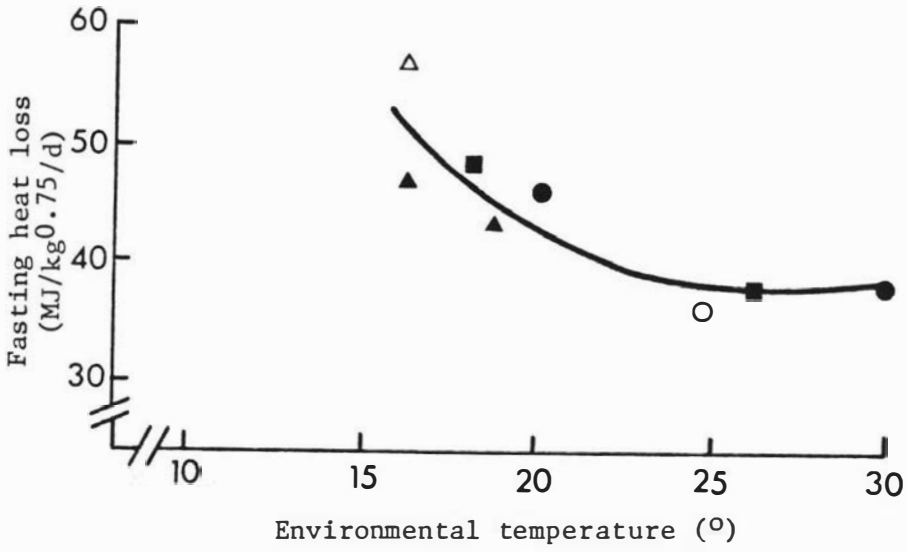
It is possible to correct for several systematic errors in determining F.H.P., by standardizing measurements of fasting energy balance, e.g. feeding the animal at a constant level (preferably maintenance) before fasting, and training the animal to its future experimental surroundings. There is a difference of opinion in the literature as to whether an increase in liveweight due to an increase in gut fill, does cause an increase in $M.E._m$ (Blaxter et al, 1966a; Van Es and Nijkamp, 1966a); the importance lies in recognizing the reference base used (see later, part 2 of this section for discussion).

F.H.P. of pigs has been measured in numerous investigations (Table 1.1, Fig.1.4); most extensive and very careful studies on F.H.P. determined in pigs weighing from 16 to 96 kg by Brierem (1936; 1939) and re-analysed by Holmes and Brierem (1974) related HP to LW by the equation:

Table 1.1 Values for the fasting heat losses for the pig maintained at various environmental temperatures, measured under different conditions (From Close and Mount, 1975).

	Conditions of measurements			
Body-wt (kg)	Environmental temperature (°)	Period after last feed (h)	Period of measurement	Heat loss ($MJ/kg^{0.75}$ per d)	Source
29-41	16.3	96-120		56.9	Deighton (1923)*
25-40	16.3	96-120	When asleep	46.9	Deighton (1929)*
105	16.9	114		38.0	Capstick & Wood (1922)*
20-60	18	96-144	24 h (mean)	47.8	Thorbek (1974)
21-33	18.7	96-120	When asleep	43.4	Deighton (1929)*
23-36	20	64-110	24 h (mean)	45.8	Close and Mount (1975)
170	23.7	84	When asleep	26.9	Capstick & Wood (1922)*
20-40	24-25	120-144		36.0	Breirem (1936)
26-60	26	96-144	24 h (mean)	38.0	Thorbeck (1974)
25-35	30	64-110		38.0	Close and Mount (1975)

*Estimated mean 24 h values for heat loss.



▲ Deighton (1929)
△ Deighton (1923)
■ Thorbek (1974)
● Close & Mount (1975)
○ Brierem (1936)

Figure 1.4 Rates of fasting heat loss (MJ/kg$^{0.75}$ per d) for pigs maintained at various environmental temperatures (°) taken from several authors (From Close & Mount, 1975).

(1) $FHP = 229\ LW^{0.512}$ which could be converted to:

(2) $FHP = 185\ LW^{0.569}$

ARC (1967) proposed:

(3) $HP = W\ (28.3e^{-0.049W} + 9.2)MJ$ for $W > 50$ kg

(4) $HP = W\ (14.2^{-0.011W} + 4.2)MJ$ for $W < 50$ kg.

Equation (3) fits very well experimental data on F.H.P. obtained for baby pigs weighing less than 10 kg (Mount, 1968; Jordan and Brown, 1970). As animals grow older, the decrease in F.H.P. per unit weight becomes less striking, and for pigs 30 to 90 kg liveweight, a straight line would fit F.H.P. data almost as closely as any exponential or other curve (see Fig. 1.5, Kielanowski, 1972a). Fig. 1.5 also shows curves for H.P. in fed animals.

The fasting metabolism per kg metabolic body weight ($W^{0.75}$) as a rule is found to be higher in growing than in mature animals (Brierem and Homb, 1972). This means that extrapolation of "k_m" from F.H.P. to ME_m (Fig. 1.3), using data from older animals may estimate ME_m accurately, but that extrapolation using data from young or growing animals might have a high error, especially in giving values which are too high for the maintenance requirement of young animals.

2. Experiments at, above or below maintenance feeding.

The quantity of energy required for maintenance can be estimated directly in fed as opposed to fasting animals, if the energy content of their food is known and their energy balance can be measured (Fig. 1.3). Where an animal is used for successive trials, the body weight of the animal is usually not equal in both a first and a subsequent trial. It is unclear whether an increase in liveweight

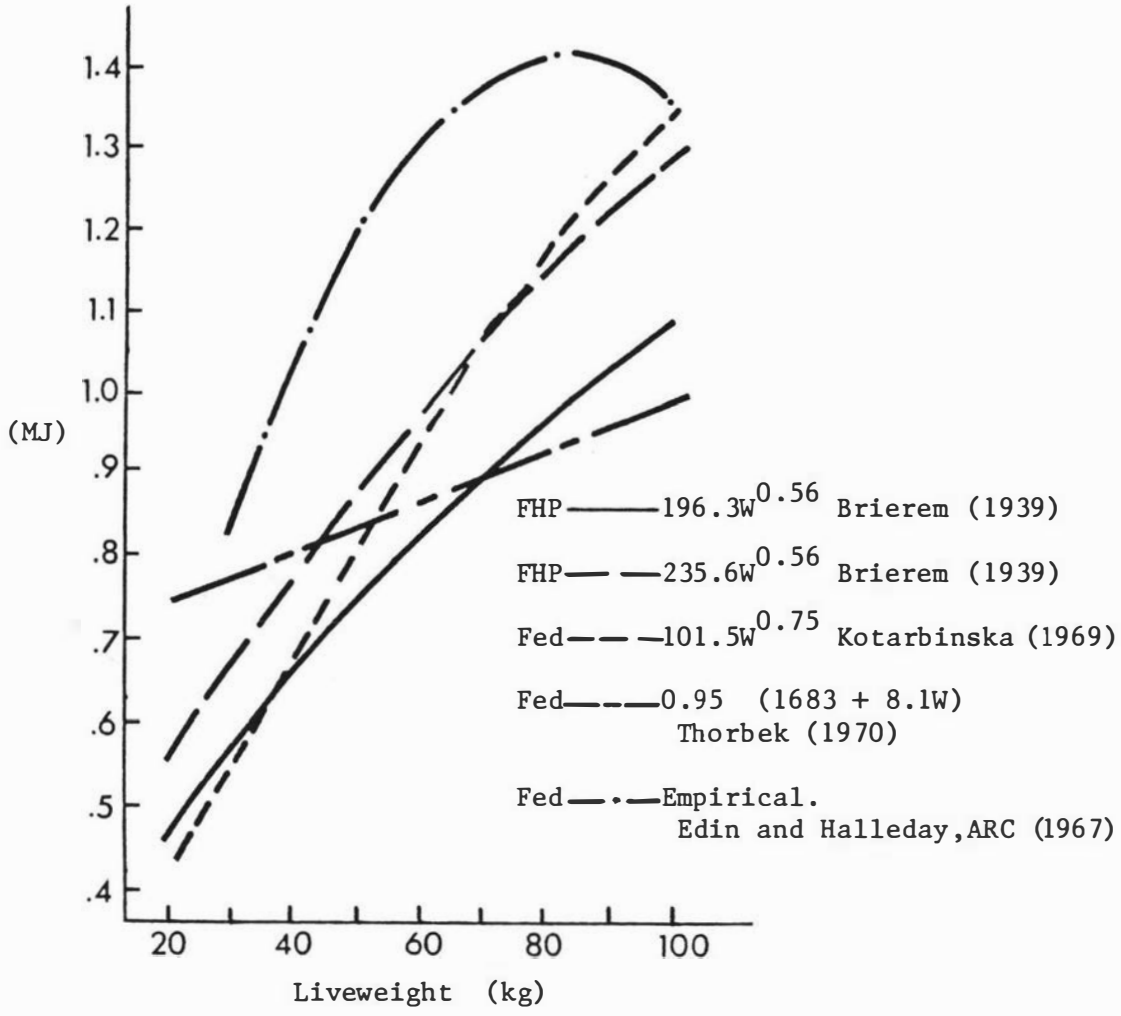


Figure 1.5 Maintenance requirement (metabolizable energy)

(From Kielanowski, 1972a)

due to greater fill of the digestive tract will change the maintenance requirement for energy; but a loss or gain of weight during the transition period between experiments certainly will. A correction term for computing k_m, or efficiency of M.E. use for fattening (k_f), may be added where research workers suspect that fill of the digestive tract changes maintenance requirement for energy.

$$k_m = \frac{EB_2 - EB_1}{ME_2 - ME_1} - a\ (W_2 - W_1)$$

where a = the increase of maintenance requirement for M.E. associated with an increase of 1kg body weight

To prevent wrong estimation of 'a', the time between the two balance trials should be as short as possible, their feeding levels should not differ too much, and animals in advanced stages of fattening should not be used in maintenance requirement determinations with this method.

Errors of k_m and k_p hardly influence the precision of the estimate of $M.E._m$ if the energy balance nearest to energy equilibrium is small. A high precision of k_m and k_f is required if $M.E._m$ is to be converted into $N.E._m$ or $N.E.F._m$. In this case, the values of k_m and k_f might be better obtained from other trials especially performed for the correct determination of k_m and k_f, or the trials might be repeated a few times while taking care that one of the energy balances was near zero and the other balance was fairly high or low (Schiemann, 1958; Nehring et al, 1961). This method is not suitable for a lactating animal but can be useful for a growing animal (Blaxter et al, 1966b).

The application of the difference (or regression) method is useful for measuring $M.E._m$ in growing animals because during growth the maintenance requirement for energy steadily increases with liveweight$^{0.75}$.

If a linear relationship exists between energy retained and the amount of energy of the food given above the maintenance requirement, then the maintenance requirement of the animal while growing may be found by extrapolating energy intake with food to zero energy retained. A linear relationship does exist between M.E. and total energy retained, at least for mature animals.

The general regression equation is:

$$ER = a \times (ME_I - ME_m)$$

where a = conversion efficiency into the product of that part of the feed consumed above computed maintenance requirement, b.

The reliability of the regression coefficient is highest when the independant variable ME_I has no measurement error, its range of use is larger and when it is responsible for most of the variation of the dependant variable (product). Factors complicating the above equation are:

1. Variation in bodyweight of the animals due to weight of tissue or fill of the digestive tract (Graham, 1964).

2. The relationship between product and feed might not be linear (Nehring et al, 1966; Blaxter, 1962).

3. Feeding above the maintenance requirement might produce more than one kind of product, or product composition might change in the course of the experiment, or might differ between values of ME_I (Kielanowski, 1964; 1966; Thorbek, 1967; Armstrong and Blaxter, 1964; Flatt et al, 1967; Henning and Kleeman, 1967).

4. The food intake might not be free from errors of determination.

5. The efficiency of utilization of $M.E._m$ and $M.E._f$ depends on the origin of these two kinds of energy.

6. The maintenance requirement of the animals might not be

constant during the trials due to variations in the course of time, or to a possible relationship between maintenance requirement and level of production (Frens, 1962).

Reliable estimates of $M.E._m$ in the growing pig need results from balance trials performed both at normal and at reduced growth rate during two or three parts of the growth period (Fig. 1.3). Growth should not be reduced completely as this might result in changes in the composition of the animal. Mitchell and Hamilton (1929) kept the body weights of 15 pigs of 20-25 kg and another 15 pigs of 100 kg constant by feeding maintenance rations. Fat was replaced by water, protein and ash, especially in the younger animals. Thus growth had obviously continued. This type of change might occur in animals where rate of liveweight gain is reduced very severely.

If, during growth, intake of M.E. is increased at nearly the same rate as $kg^{0.75}$ body weight, or there is effectively only one level of feeding, in such cases it is very difficult to separate requirement for maintenance from those for production.

The errors of the predictions for maintenance and production compensate each other so that they hardly increase the residual standard deviations of the regressions. No reliable estimate of maintenance can be made by extrapolation unless the variation between the ratio of M.E. and $bodyweight^{0.75}$ is high (Van Es, 1972), that is, unless the level of M.E., at a particular liveweight, varies widely (Fig. 1.3).

3. Long-lasting feeding trials.

Animals in these trials are maintained at constant body weight by adjusting the feed intake where necessary. Feeding trials for

measurement of total requirements are very useful; their total error is not high, provided they are conducted for a long time in the correct way. The feed intake of the animals are determined, and digestibility and metabolizability of the food is determined with some of the animals used (Van Es, 1972a). Two main sources of error might affect the precision of the result. Firstly, small changes in body weight are difficult to measure with sufficient precision, mainly due to the irregular pattern of excretion of faeces and urine, e.g., Mollgaard (1929). Garret et al, (1959) describe a case where steers gained liveweight but lost energy. The energy content of the body weight gained or lost may vary considerably depending whether the loss or gain comprises fat, protein or water. This means that it is not easy to correct the feed intake in such a way that no energy change occurs. The influence of this kind of error may be diminished by increasing the number of animals and length of trial.

The second source of error is that while feeding rations for long periods, the estimation of the total quantity of digested food may be wrong due to undetected systematic errors. The influence of this sort of error can only be decreased by working very accurately and by performing digestibility trials with the animals themselves.

This type of experiment is unsuitable for lactating animals, owing to the mobilisation of body tissue that normally would take place; it is also unsuitable for young growing animals, owing to the long duration of the trials at a low level of feeding.

4. Prediction of maintenance requirements and their use in practice.

Few animals (other than breeding stock) are kept at maintenance for long periods of time. The need, therefore, is great for

data which apply to maintenance in a producing animal. Fasting and maintenance results may only be used as such if it has been proven that no difference exists between these results and those results obtained with the regression method, given that the regression has no systematic errors.

One systematic error,which is inherent,lies in the fact that during measurements the animals must be kept in the exceptional circumstances of a balance trial. Also, the relatively short duration of such balance trials is often considered a second possible source of error. With animals of a short life, i.e. stock for meat production, carrying out a number of balance trials throughout the whole growth period with the same animals minimizes error (Van Es, 1972a).

1.4.2 Factors which exert major influences on the Maintenance Requirement for Energy, $M.E._m$.

1. The influence of body weight.

In experiments measuring F.H.P. using animals of different species varying in weight Rubner (1883) and Voit (1901) found that results for animals of widely different weights varied little if expressed per $metre^2$ body surface. Brody (1945) and Klieber (1965) related F.H.P. to body weight, giving values of 0.73 and 0.75 respectively as the power of the body weight (W) in the equation. Statistically the difference between the two values is not significant, but if F.H.P. is expressed in kcal per kg bodyweight to the power 0.73 or 0.75, this results in a considerable difference in the constant preceding the power function. It is not certain whether a power, satisfactory for F.H.P., is also satisfactory for the energy requirement at maintenance or for production.

Especially at low body weights (W),the slopes of the exponential

functions $W^{0.6}$, $W^{0.75}$ and $W^{0.9}$ change much more rapidly than at high values of W (Table 1.2).

Table 1.2 Changes in exponential function (W^n) with a change in bodyweight (W)

W	$W^{0.6}$	$W^{0.75}$	$W^{0.9}$	$\frac{d(W^{0.6})}{dW}$	$\frac{d(W^{0.75})}{dW}$	$\frac{d(W^{0.9})}{dW}$
25	6.9	11.2	18.1	0.17	0.34	0.65
50	10.5	18.8	33.8	0.13	0.28	0.61
100	15.8	31.6	63.1	0.10	0.24	0.57
200	24.0	53.2	117.7	0.07	0.20	0.53
400	36.4	89.4	219.7	0.05	0.17	0.49
800	55.2	150.4	410.0	0.04	0.14	0.46

Thus, if 0.75 is the 'correct' exponent for $M.E._m$, then $M.E._m/kg^{0.75}$ for a 30 kg pig will be equal to $M.E._m/kg^{0.75}$ for a 100 kg pig. However, if 0.6 is the correct exponent, but $M.E._m$ is still expressed per $kg^{0.75}$, then the value for a 30 kg pig will not be equal to that for a 100 kg pig. This sort of error may give rise to a maximum error of 11% for a pig at either end of the weight range 25 to 100 kg, compared with a pig of 38 kg.

The choice of power is therefore more important for young growing animals than for mature animals.

2. The influence of composition of the ration.

Most investigators agree that the animal body requires mainly free energy for its maintenance (Blaxter, 1962; Nehring and Schiemann, 1966; Klieber and Black, 1966). The main substance which is used as a source of free energy in the animal is adenosinetriphosphate

(A.T.P.). If A.T.P. production is given as 100 units per M.J. of M.E. as fat, the relative A.T.P. production of other substances per M.J. are 102 units for glucose and 82 units for casein. In animals fed orally, the additional supply of free energy needed for eating, chewing, ruminating and digesting is considered to be small (Blaxter, 1962; Baldwin, 1968), but it probably increases with a higher degree of coarseness of the feed. It is probable that in non-ruminants which eat concentrated feeds the act of eating will require only very small amounts of energy, except when they have exceptional eating habits. It seems probable that in non-ruminants with normal eating habits, there are only very small effects of composition of absorbed nutrients on the amount of M.E. required for maintenance. M.E. given as protein is probably utilized 15-20% less efficiently than M.E. given as glucose or fat. The contents of digestible protein in pig rations seldom vary by more than 15-20% crude protein in the diet. Thus differences of 3-4% in efficiencies of M.E. utilization of the rations may be expected. It is, however, very difficult to prove the existence of such small differences experimentally.

3. The influence of age.

Training the young animal to circumstances of a trial will take more time than is the case with a mature animal, because young animals are generally more active and react in a more vigorous way to new circumstances (Van Es, 1972a). The necessary feeding at maintenance level prior to the fasting period might result in the animal being under some degree of stress. The composition of growing animals changes with age. Water and protein contents decrease, while fat content increases. Therefore, the power 0.75, which generally

applies to all kinds of mature animals, need not necessarily also apply to growing animals. This makes correct interpretation of results very difficult (Van Es, 1972a).

4. The influence of environmental temperature.

The animal produces additional heat by physical and chemical means when its heat production is not sufficient to be equal to the loss of heat via the lungs and skin. The temperature below which this occurs is called the (lower) critical temperature. Wind and rain which adversely affect the insulation of the animal may increase this critical temperature (Blaxter and Wainman, 1966a). As the efficiency of M.E. utilization for maintenance and production is always below 100%, feeding causes an increase in heat production. Thus the critical temperature will be lower for the animal on a high level of feeding. The results of studies of environmental physiology will depend on the feeding level used, on the animal's environment and on the animal's physical insulative properties. When determinations of maintenance requirement are being made, the animal's heat production should not be influenced by the climatic environment, that is, the animal should be kept in thermoneutral conditions.

5. The influence of between-animal variation.

If temperament and nervousness can influence the maintenance requirement, it seems probable that the same animal in the course of time may change its requirement due to its reaction to a new environment, new attendants or a changed way in which it is kept, called period variation (Mollgaard, 1929). In 237 results of balance trials, Van Es (1961) compared the total variation of the corrected results and their within-animal variation. It was concluded that the

between-animal variation amounted to 5-10% of the average maintenance requirement, part of which was caused by differences in requirement between breeds (Van Es, 1972a).

Van Es and Nijkamp (1967) showed that variation could arise from insufficient training of animals to the environment of balance trials. Endocrine relationships may influence the maintenance requirement, and further evidence of variation between animals has been provided by Schiemann et al (1961a), Nehring et al (1961) and ARC (1965) with cattle, and Graham (1967) with sheep.

1.4.3 Estimates of the maintenance requirement for energy from experimental results

There is a considerable amount of information about the energy metabolism of pigs ranging from birth to 100 kg, and some information about the energy metabolism of sows. Holmes and Close (1977) presented results from various authors, analysed in relation to live-weight and age of pigs, their intake of M.E., and the effects of pregnancy in sows.

Values in Table 1.3 represent mean values for the particular conditions, and H.P. at maintenance equals $M.E._m$ in this table.

The results show a general decline in heat production per $kg^{0.75}$, with increasing age; but an increase in heat production with pregnancy for sows, especially towards the termination of pregnancy.

Further values presented by Holmes et al (1980) for heat production at maintenance were:

	$M.E._m$ (when ER=0) with pigs 30-90 kg
Boars	0.43 (MJ per $kg^{0.75}$ daily)
Barrows	0.48
Gilts	0.44

Table 1.3 Heat production, under thermoneutral conditions, of pigs at several liveweights and fed on different amounts of energy (From Holmes & Close,1977)

	Metabolisable energy intake			
	0	M[1]	2M	3M
Type of pig	Heat production (MJ per $kg^{0.75}$ daily)			
MILK-FED				
Newborn	0.531	0.573	0.640	0.707
Young	0.406	0.494	0.565	0.636
SOLID-FED				
Young		0.649	0.795	0.941
20-50 kg	0.397	0.423	0.561	0.699
50-100 kg	0.364	0.410	0.527	0.644
SOWS				
120-180 kg		0.393	0.531	0.699
PREGNANT SOWS				
60 days		0.456	0.594	0.732
112 days		0.510	0.653	0.787

[1] M = metabolised energy required for maintenance; assumed to be 0.42 MJ ME per $kg^{0.75}$ daily.

Equations derived from results from various workers are depicted in Fig. 1.6. They show good agreement for different workers, but also a difference in $M.E._m$ for two breeds of pig.

1.5 Energy Requirements for Growth

Energy Metabolism is much more difficult to investigate in growing animals than in adults. Maintenance Requirement ($M.E._m$) of adult animals is clearly defined and can be measured precisely, but in experiments with growing animals $M.E._m$ cannot be separated easily from the requirement for increment of body substance. Energy Retained (E.R.) during growth is a direct measure of the requirement for N.E. which must be supplied in the ratio above $M.E._m$. The quantity of protein laid down must be differentiated from that of fat. Protein produced contributes more weight (kg) to liveweight gain per unit energy laid down than does fat (Van Es, 1972), discussed earlier in section 1.3. Further, the amount of protein deposited in the tissues of growing animals, although quite large in terms of weight, is relatively small in terms of energy deposited as protein, and is not easily varied by experimental means. For that reason, the energy cost of protein synthesis or storage cannot be determined directly (Kielanowski, 1972a).

Until recently, therefore, energy requirements of growing animals had to be based on purely empirical evidence.

However, data on the chemical composition of growing animals have been accumulating (Oslage, 1962b; Kotarbinska, 1969), and this encouraged several investigators to estimate energy costs of deposition of organic compounds in the body by statistical methods (Kielanowski,

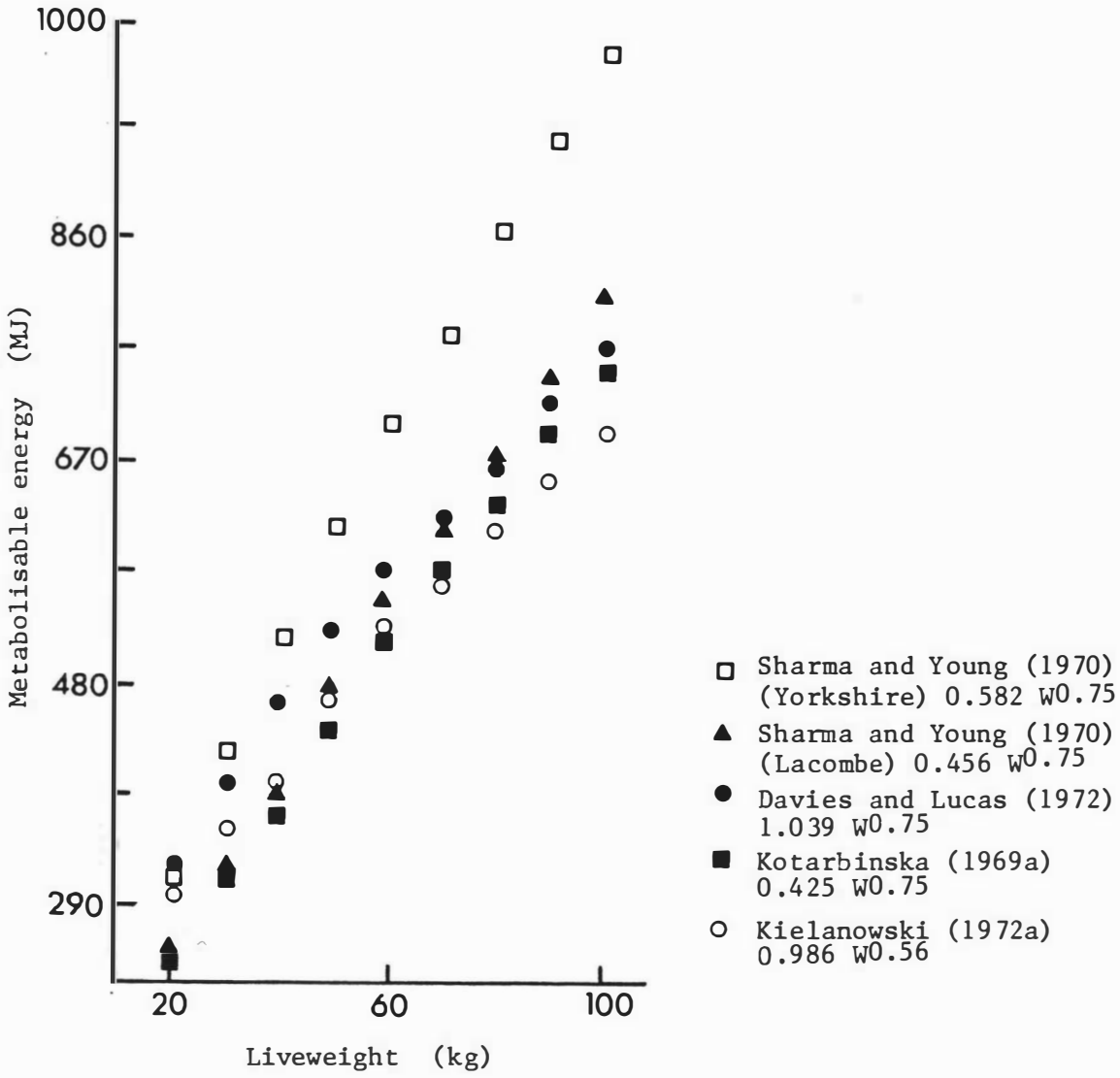


Figure 1.6 Maintenance requirements (ME) of growing pigs.

(From Cole, 1974)

1972a), i.e. by a form of mathematical partitioning of M.E. which cannot be achieved experimentally. Kotarbinska and Kielanowski (1967) and Kielanowski (1972a) did this with pigs growing between 20 and 90 kg. Their model provided no information concerning the utilization of M.E. below maintenance but, however, this is of no particular practical interest for the growing pig. There are several widely recognized statistical shortcomings. First, it is difficult to ensure that the independant variables are not closely correlated with each other, e.g. daily lipid accretion may be positively or negatively correlated with daily protein accretion. Secondly, the model assumes that the efficiencies of protein and lipid deposition are constant over a wide range of stages of maturity, regardless of the rate of accretion; i.e., it is essentially a linear model (Fowler, 1978).

Also, much attention has been given lately to the $M.E._m$ of growing animals (Brierem, 1971), and so attempts can be made to describe their total energy metabolism in physiological terms (Chamberlain, 1972).

In the example given below, the M.E. derived from the diet (26.8 MJ; Fig. 1.7), is partly retained as protein (2.4 MJ) and fat (7.9 MJ) stored in the body, and partly dissipated as heat (16.5 MJ), (Kielanowski, 1972a).

Greater protein deposition often results from a higher content of protein in the ration. It could be deduced, therefore, that the costs of assimilation of feed protein enter into the account of the energy cost of protein deposition, though the finding (Zebrowska and Buraczewska, 1972) that the amount of endogenous nitrogen secreted into the pig's gut is practically independent of the protein concentration

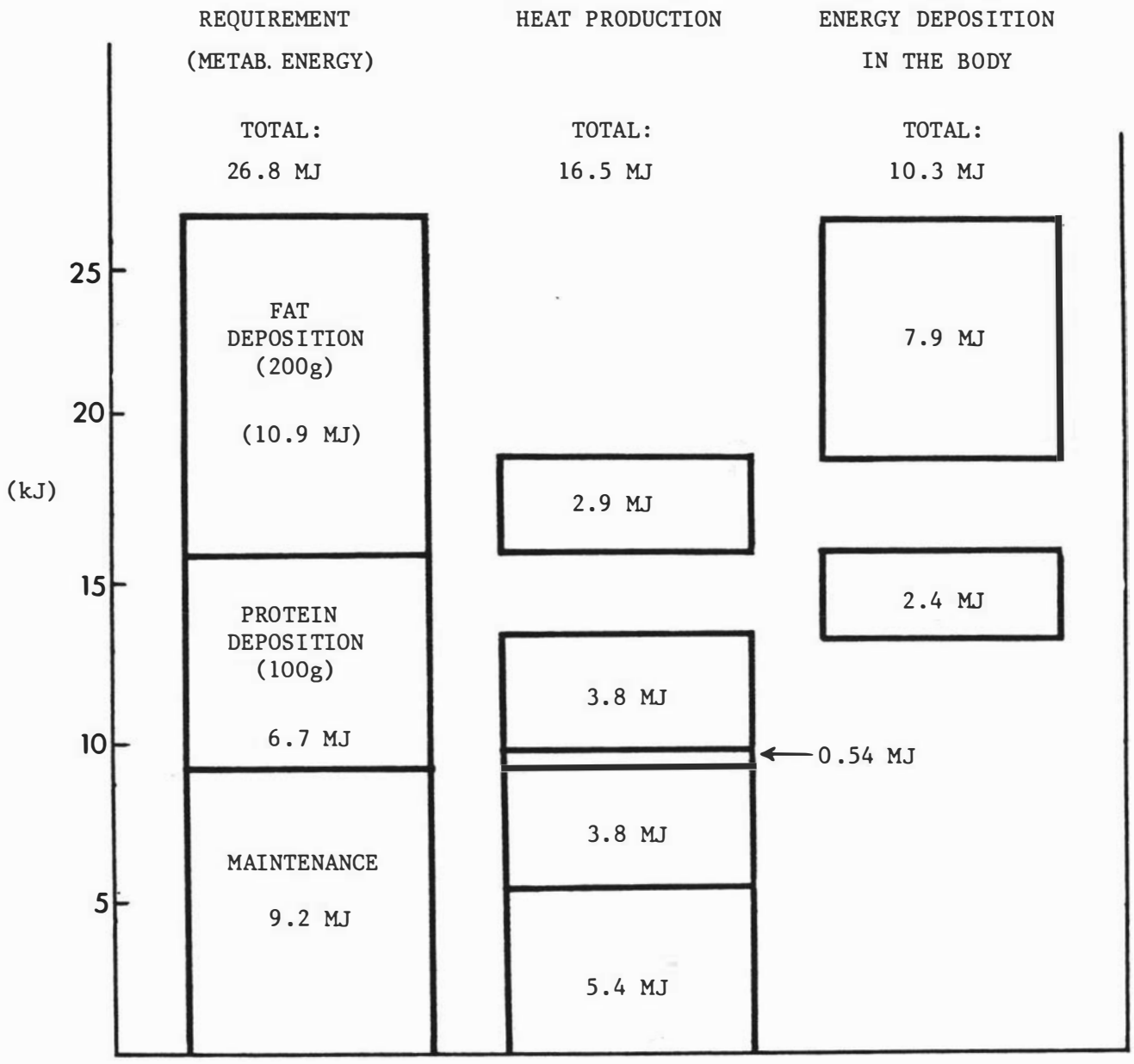


Figure 1.7 Energy balance of a growing pig (Liveweight 60 kg, daily gain 0.65 kg). In heat production, dark blocks represent the constant fraction and clear blocks, the fraction depending on the composition of the ration (From Kielanowski, 1972a).

in feed, does not support this supposition. Since protein synthesis would not go on at any site if all amino acids needed were not present in the right proportion, and since the loss of urea caused by deamination of superfluous amino acids is accounted for by the determination of M.E., it seems that the energy cost of protein deposition should not depend on the quality of feed protein (Kielanowski, 1976). However, premises for this conclusion may not be adequate. Investigations by Thorbek (1970) suggest that the variance in energy loss due to utilization of poor quality protein may be important.

In the growing pig, as much as 60% of M.E. is lost as heat. Heat is lost owing to different physiological processes (see previous section). The M.E. system for describing the energy requirements of ruminants, explained in detail by Blaxter (1967), and depicted in Fig. 1.7, attributes heat production to three components: firstly, the fasting metabolism, 5.4 MJ, expenditure of energy (derived from high-energy bonds) for the true work of maintenance, and secondly, for protein synthesis, 0.54 MJ. For this example, it is assumed that this fraction depends on the pig's liveweight and the amount of protein deposited, and does not depend on the kind of ration. The remaining (third) fraction of heat production (H.P.) results from energy costs of assimilation and conversion of nutrients included in animal feed, and therefore, depends on the composition of the ration, 3.8 MJ, 3.8 MJ and 2.9 MJ.

In some cases, this fraction is considerably reduced, e.g. H.P. connected with fat deposition seems to be negligible in milk-fed baby pigs (Jordan and Brown, 1970; Kielanowski and Kotarbinska, 1970). In other cases, e.g. when the concentration of protein or roughage

in the ration is very high, the heat loss dependant on ration composition is increased. In the energy balance diagram, the partitioning is symbolic of the part of H.P. which is variable due to ration composition into portions connected with $M.E._m$ or the deposition of protein or fat. Various substrates are taken for each purpose from the same common pool. Investigations have shown that the live weight of animals and the amounts of protein and fat deposited daily in their bodies appear sufficient to predict fairly accurately their total energy requirements (Kotarbinska, 1969). Energy cost of deposition of mineral matter is negligible; 'work of growth' has not been considered here either. It can be supposed that the tranformation of nutrients into a complex organism involves an expenditure of energy, which should be added to the bare cost of chemical synthesis (see Brody, 1945); the statistical approach precludes this ambiguous question, because if the 'work of growth' increased H.P., it would be included in the costs of protein deposition and fat deposition.

The H.P. denoted by clear blocks in Fig. 1.7 varies depending on the composition of the diet and on the use to which the diet is put by the animal's metabolic reactions. Requirements for energy must also vary accordingly (Kielanowski, 1972a).

1.5.1 The partition of metabolizable energy from birth to slaughter

Comprehensive data predicting the partition of M.E. at any stage of growth are not available. Kotarbinska and Kielanowski (1969) provide values which are integrated over one particular period of growth. Cumulative protein and lipid accretion from birth to 140 kg and total heat loss are indicated in Fig. 1.8 using data from Fowler

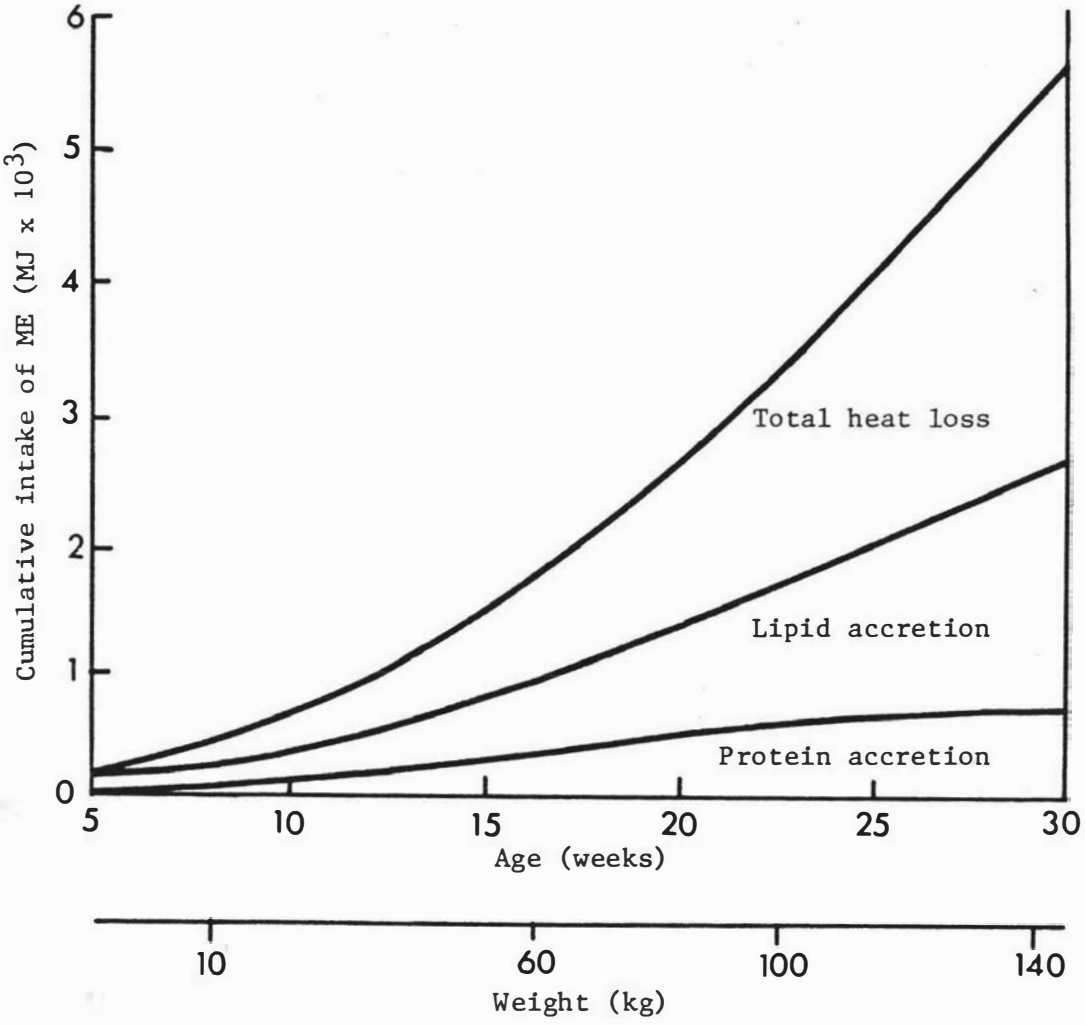


Figure 1.8 Partition of cumulative metabolizable energy during growth between heat loss and the accretion of protein and lipid (From Fowler, 1978).

and Livingstone (1972), Oslage and Fliegel (1965), Close and Mount (1975) and Thorbek (1975). The inflection in the curve of protein accretion occurs at about 65 kg liveweight and that in the curve of fat accretion at about 105 kg liveweight. No feeding scales were quoted for the model.

It is immediately obvious from Fig. 1.8 that the energy retained as protein becomes progressively smaller as the animal matures. This model gives a description of energy partition with changing time, but it is still relatively static.

A tentative model, accomodating changes in feed intake, but based on limited data and referring largely to growth from 30 to 90 kg was constructed by Fowler (1978). This was based partly on work of Black (1974) who attempted a similar exercise with daily M.E. intake of lambs, (Fig. 1.9).

The model assumes a pig at 60 kg given a balanced diet with adequate amino acid composition and eating close to its appetite at a rate of 31.5 MJ/day could accrete a maximum of 137.5 g protein per day. This value corresponds to 22g/day of nitrogen retention, which is at the higher end of the values in the literature reviewed by Thorbek (1975). Data from the same source, from Close (1977) and from Fuller et al (1976) were used to set the daily nitrogen retention at zero energy balance to 5g and the initial nitrogen loss when fasting to 5g/d. The maintenance requirement was taken as 0.44 MJ/kg $W^{0.75}$. Using simplified values for k_f and k_p, the efficiency of utilization of M.E. for lipid accretion and protein accretion respectively, as $K_f = 0.75$ and $k_p = 0.40$, the partition above maintenance was then calculated. An arbitrary value of 0.8 was taken for k_m. To examine whether such a model could be validated by direct experimental data, the data of

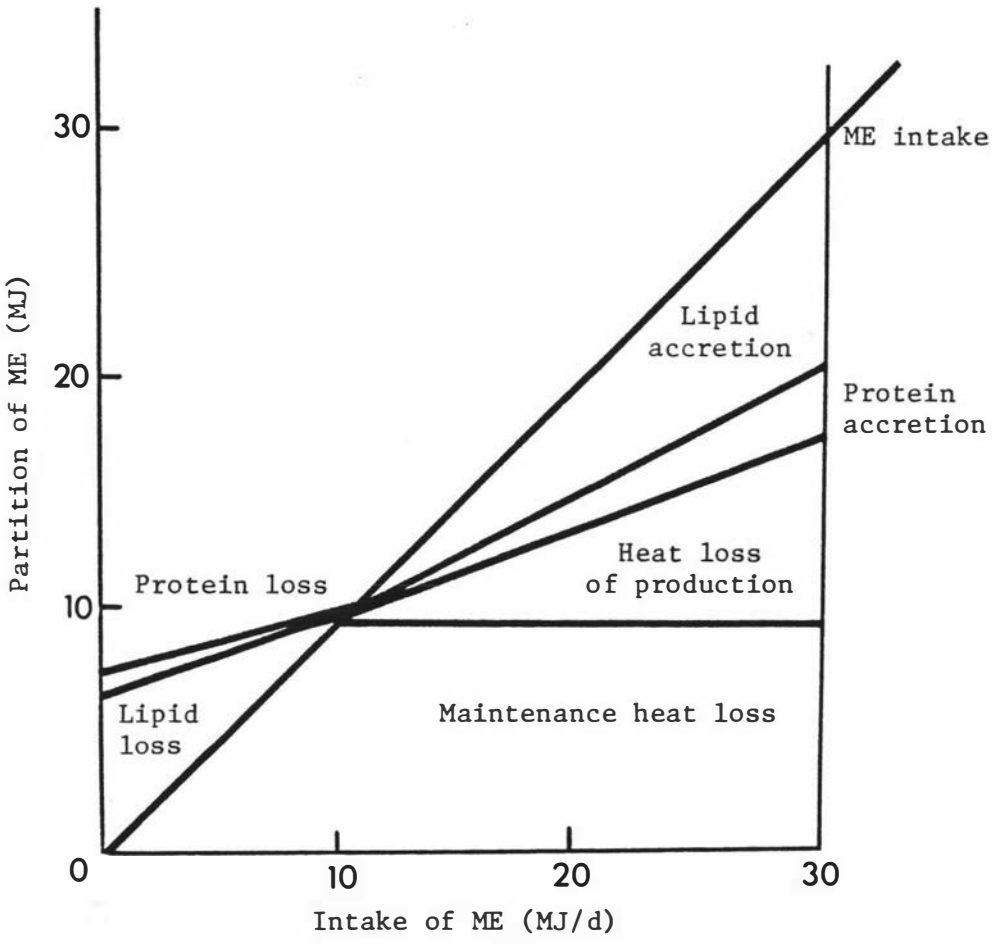


Figure 1.9 Partition of metabolizable energy at different rates of daily intake for a pig of liveweight 60 kg (From Fowler, 1978).

Fuller and Boyne (1971a; b) were used. Data were for pigs in a thermoneutral environment, and nitrogen balance data was adjusted for discrepancies between metabolism cage balances and comparative slaughter. The comparison is set out in Table 1.4

Table 1.4 Comparison of results predicted from the model shown in Figure 1.8 and actual results calculated from the data of Fuller and Boyne (1971a,b) (From Fowler,1978)

		Intake of ME (MJ/d)		
		19.6	23.8	28.8
Heat loss per day (MJ)	Model	13.4	14.7	16.1
	Actual	12.2	13.4	14.8
Energy retained as protein per day (MJ)	Model	1.7	2.3	3.0
	Actual	2.4	2.9	3.5

1.5.2 The energetic efficiency of growth

The efficiency with which the growing animal converts the food it eats above maintenance into fat and protein is determined overwhelmingly by the efficiency with which it uses the major nutrient, which is energy. During uninterrupted growth, body weight and other related parameters such as lean mass, body fat content and metabolic rate increase from the time of conception, or shortly after, along curves that proceed in a sigmoid fashion to an asymptotic value which is reached at maturity (Webster, 1980). Fig. 1.10 illustrates approximately the efficiency of utilization of M.E. by an animal as it proceeds from weaning to maturity.

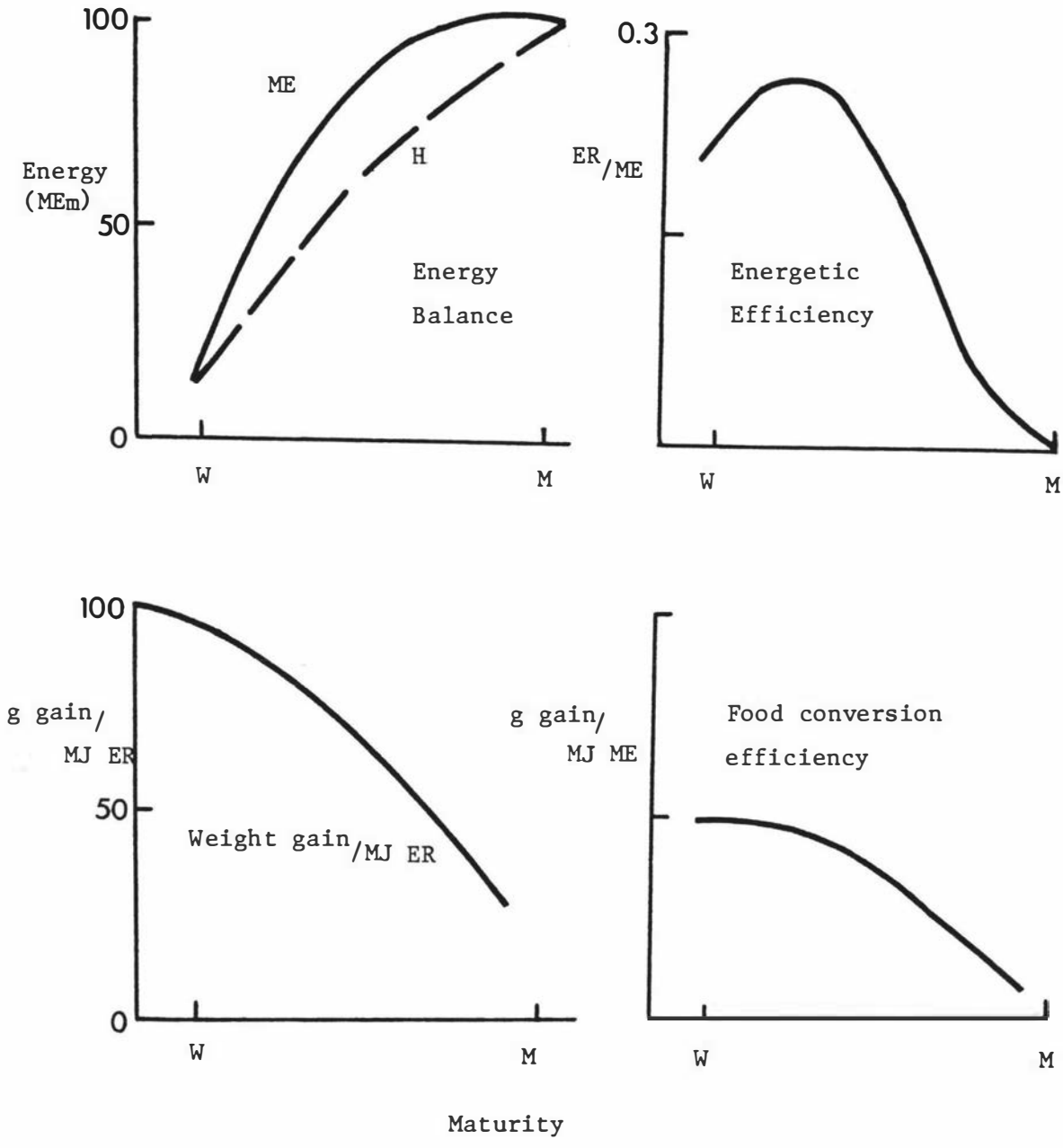


Figure 1.10 Factors affecting the efficiency of utilization of metabolizable energy (ME) for growth. ER is energy retention, H is heat production. W and M are weights at weaning and maturity, respectively. ME_m is maintenance requirement at mature body weight (From Webster, 1980).

During growth, M.E. exceeds H.P. As the animal matures, these two values converge (Fig. 1.10.1). Overall efficiency of energy retention (k) in this example reaches a peak at about 25% of mature body weight and declines steeply thereafter (Fig. 1.10.2). As an animal matures the ratio of fat to protein in the body gains increases (Webster, 1980). The energy content of lean meat is about 4.8 kJ/g and for fat it is about 30 kJ/g (Kielanowski, 1972a). Thus the ratio of weight gain (g) to E.R. (M.J.) declines throughout growth (Fig. 1.10.3). Finally, feed conversion efficiency, which reflects both k/M.E. and the energy content of the body gains, is relatively constant during the first third of growth and declines steeply thereafter (Fig. 1.10.4). Maturity therefore dominates the energetic efficiency of growth (Webster, 1980). The results of manipulation of growth by nutrition or selection can only be validly compared by having animals at the same stage of maturity.

Close (1978) determined the partial efficiency of energy retention above maintenance (k). He concluded that k decreased with environmental temperature from 0.79 at 10°C, to 0.63 at 30°C, with 0.67 at the thermally-neutral temperature of 25°C. Analysis within several ranges of environmental temperature suggested a curvilinear relation between ER and ME_I, indicating a decrease in k with increase in level of feeding, particularly at thermally-neutral temperatures (Table 1.5).

Holmes et al (1980) investigated the energy and nitrogen metabolism of boars, barrows and gilts at 30 and 90 kg liveweight fed two diets and determined values for k by regression of ER on ME_I. (M.J./$kg^{0.75}$/day) (Table 1.6).

Table 1.5 The partial efficiency of energy retention (k) over several ranges of metabolizable energy (ME) intake at environmental temperatures equivalent to 12.5, 22.5 and 30° (From Close, 1978).

Environmental temperature (deg)	Ranges of ME intake ($kJ/kg^{0.75}$ per d)			
	0-400*	400-800	800-1200	1200-1600
12.5	0.96	0.80	0.82	0.75
22.5	0.95	0.75	0.65	0.68
30	0.77	0.68	0.60	-

* Values calculated on the basis that the fasting heat loss at 12.5, 22.5 and 30° was 573, 418 and 380 $kJ/kg^{0.75}$ per d, respectively. These were calculated on the basis that the fasting critical temperature is 25° and that fasting heat loss increases by 15.4 $kJ/kg^{0.75}$ per d per 1° below the critical temperature.

Table 1.6 Results of regression analyses of energy retained (E.R.) on metabolizable energy ($M.E._I$) ($MJ/kg^{0.75}/day$). (From Holmes *et al*, 1980).

	Pooled	Diet 1	Diet 2
Gilts	0.62	0.63	0.62
Boars	0.57	0.64	0.50
Barrows	0.68	0.69	0.66

Comparison between these sets of data at a particular and common value for ME_I, an intake of 1.12 MJ $ME/kg^{0.75}$ per day, puts the results of Holmes *et al* (1980) slightly lower than of Close (1978) at 25°C and consistently lower than those of Fuller and Boyne (1972).

1.5.3 The energetic efficiency of fat deposition

Estimates of k_l for lipid accretion usually lie between 0.65 and 0.83 across species but values for the pig remained fairly consistently in the narrower range of 0.77 to 0.70 (Fowler, 1978) as indicated by Table 1.7.

Table 1.7 Estimates of the energetic efficiencies of protein (k_p) and fat (k_f) synthesis in the pig, compiled from various sources. (From Close, 1978).

Body-wt	k_p	k_f	Source
2-9	0.76	0.81	Kielanowski (1965)
20-90	0.35	0.73	Kotarbinska (1969)
20-90	0.43	0.77	Thorbek (1970)
25-110	0.52	0.70	Oslage, Gädeken & Fliegel (1970)
25-45	0.47	0.69	Close & Mount (1971)
5-25	0.76	0.78	Burlacu, Baia, Ionila, Moisa, Tascenco, Visan & Stoica (1973)
20-40	0.58	0.70	Close, Verstegen & Mount (1973)
30-110	0.52	0.70	Gädeken, Oslage & Fliegel (1974)
20-90	0.48	0.77	Thorbek (1975)
9-58	0.66	1.00	Burlacu, Illiescu & Stravi (1976)
20-50	0.71	0.71	Close (1978)

Schiemann et al, (1961) calculated that the energy from dietary fat is incorporated into accreted fat with an efficiency of 0.86, while that from dietary carbohydrate and protein are 0.76 and 0.66 respectively. On this basis, a conventional cereal-based ration containing 80% of its energy as carbohydrate, 15% as protein and 5% as fat would be expected to have a k_f value of 0.75, indicating an M.E. requirement for

synthesis of 53 kJ/g (Close, 1978). The figure for M.E. requirement for fat storage in adult pigs fed a ration composed mainly of grains and protein supplements is also quoted at about 0.73 to 0.74 MJ fat stored per 1M.J.M.E. by Kielanowski (1972a). Thus the M.E. cost of storage of 1g fat (calorific value 39.6 kJ) is about 53.5 - 54.2 kJ. An addition of fat to the diet would improve M.E. utilization, since some of the fatty acids absorbed from feed would be stored at practically zero energy cost (Schiemann, 1969).

Kotarbinski (1969) obtained an estimate of 54 kJ M.E/g fat deposited in baby pigs, which indicates that the energy cost of fat deposition in growing animals is exactly the same as in adults (Kielanowski, 1972a), (Table 1.8).

Table 1.8 Metabolisable energy expended in fat deposition found from energy balance experiments (From Buttery and Boorman, 1976).

Animal	Energy cost (kJ/g) Fat	Source
Piglet	48.7	Kielanowski, (1965)
Growing pig	56.3[1]	Kotarbinska and Kielanowski (1969)
Growing rat	55.6[2]	Schiemann et al (1969)
Piglet (re-calculated)	54.2[1]	Kielanowski and Kotarbinska, (1970)
Growing pig (re-calculated)	-	Ibid
Growing pig	51.9	Thorbek, (1970)
Growing pig	55.6[2]	Oslage et al (1970)

[1] values with the same superscript were calculated from the same original data

[2] assuming energy content of deposited fat to be 38.9 kJ/g.

Kielanowski and Kotarbinska (1970) recalculated data for piglets by a modified procedure which assumed a 100% conversion of dietary fat to body fat. They previously related H.P. to fat deposition and found that statistically the relationship was negligible.

The energy cost of fat synthesis predicted from experimentation accords closely with that calculated on a theoretical basis (Schiemann, Hoffman and Nehring, 1961; Blaxter, 1962; Armstrong, 1969).

1.5.4 The energetic efficiency of protein deposition

Values for k_p ranged much more widely than k_l for pigs (Table 1.9) with estimates for other species also falling within this range. Kielanowski (1972a; 1976) and Buttery and Boorman (1976) have discussed the energy cost of protein synthesis, including the discrepancy between theoretical and predicted values.

Table 1.9 Estimates of the energetic efficiencies of protein (k_p) and fat (k_f) synthesis in the pig, compiled from various sources (From Close, 1978).

Body-wt (kg)	k_p	k_f	Source
2-9	0.76	0.81	Kielanowski (1965)
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25-110	0.52	0.70	Oslage, Gädeken & Fliegel (1970)
25-45	0.47	0.69	Close & Mount (1971)
5-25	0.76	0.78	Burlacu, Baia, Ionila, Moisa, Tascenco, Visan & Stoica (1973)
20-40	0.58	0.70	Close, Verstegen & Mount (1973)
30-110	0.52	0.70	Gädeken, Oslage & Fliegel (1974)
20-90	0.48	0.77	Thorbek (1975)
9-58	0.66	1.00	Burlacu, Illiescu & Stravi (1976)
20-50	0.71	0.71	Close, (1978).

The range of estimates of k_p proposed from various investigations are all much lower than those of 0.75 - 0.94 calculated on theoretical grounds by Blaxter (1962), Schiemann (1963), Armstrong (1969) and Schiemann, Chudy and Herceg (1969). Theoretical calculations presuppose an ideal dietary supply for tissue synthesis where all amino acids are assumed in their correct proportions. However, no allowances have been made for the energy cost of synthesizing non-essential amino acids or deaminating amino acids surplus to requirements, as may occur under normal feeding practices. This may result in a lower than theoretical estimate of k_p.

Various hypotheses have been proposed for the wide range of predicted estimates of k_p. These include differences in technique, variation in body-weight with heavier animals having lower efficiencies, variations in dietary energy and protein concentrations and differences in the method of determination (Kielanowski, 1972; Pullar and Webster, 1974; 1977a; Thorbek, 1975). Close (1978) suggests variation in estimates of k_p may also be largely attributable to differences in feeding level of animals; an interdependance between $M.E._m$ and k_p is indicated (Pullar and Webster, 1974; Kielanowski, 1976). It is also possible that a decrease in k_p may be indicative of an increase in the mean rate of protein turnover associated with both a higher rate of synthesis and a greater body protein mass of the animals at the higher levels of food intake (Tschudy *et al*, 1959; Millward *et al*, 1976; Steffee *et al*, 1976).

Although attempts to differentiate between the cost of lipid and protein accretion are theoretically extremely interesting, the gain in precision is small compared with models using only one term, k_g, for the efficiency of retention of energy above maintenance (Fowler, 1978).

The real significance or meaning of the k values remains uncertain, and the calculations represent "mathematical partitioning".

It appears that there may be a demand for a minimum rate of fat retention which relates to a "physiologically essential" level of fat in the body of the growing pig. It has been suggested that this minimum bears an approximately 1:1 relationship with protein retention (Kielanowski, 1966; Whittemore and Fawcett, 1976; Whittemore, 1977), (see Fig. 1.11). This implies that even a slow rate of protein synthesis cannot take place in the absence of some fat synthesis. Further increments of fat growth are related to the superfluity of nutrient supply in relation to the animal's demands for maintenance, cold thermogenesis and protein growth (Fig. 1.11).

In growing pigs, the rate of lipid accretion usually exceeds that of protein by about twofold. Even when pigs are growing quite slowly, the ratio of the rates of accretion of protein and lipid is rarely below 1:1. This means that the most k_g could vary due to variation of the ratio is from about 0.57 to 0.63, or approximately 10% (Fowler, 1978).

First attempts to determine the energetic efficiency of protein deposition were made experimentally by Brierem (1939) and statistically by Kielanowski (1965). The hypothetical energy expenditure for protein synthesis was deduced by Blaxter (1962) and Schiemann (1963) (Table 1.10).

Regression equations represent simply a line fitting a set of data most closely (Kielanowski, 1976); ascribing to the regression coefficients any actual physiological or biochemical meaning in isolation of experimental conditions, can be misleading. Hence, estimates of the unitary energy cost of protein deposited (E.C.P.D., which corresponds to

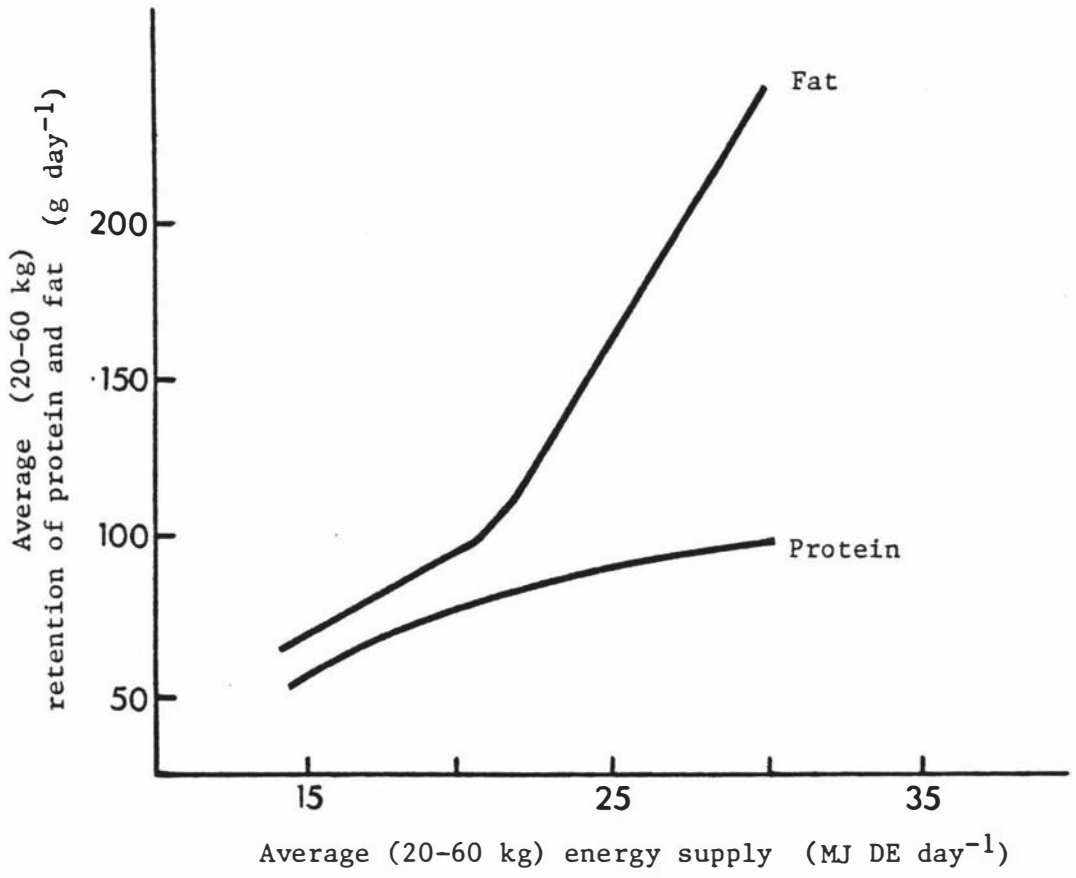


Figure 1.11 Retention of protein and fat in response to increasing energy supply (From Whittemore, 1977).

Table 1.10 An estimate of the cost of protein deposition (from biochemical deductions: Kielanowski, 1972a).

No. high-energy bonds for formation of 1 peptide bond	8 - 12
No. moles high-energy bond for formation of 100g casein	7.3 - 11.0
Free energy cost of 100g casein (at 48 kJ/mole high-energy bond	351 - 529 kJ.ME.
Efficiency of M.E. use for formation of a high-energy bond (assumed)	0.6
M.E. cost for synthesis 1 g protein	5.85 - 8.82 kJ.ME.
Calorific value of 1g protein	23.8 kJ
Minimum cost of deposition 1g protein	29.6 - 32.6 kJ.ME.

1g of nitrogen x 6.25 retained), together with factors expressing costs of fat deposition and maintenance, have limitations in that they are multipliers helping to compute total energy requirement of the animals in that particular experiment (Kielanowski, 1976). Tables 1.11 and 1.12 present some of these estimates.

Table 1.11 Estimates of the energy cost of crude protein deposition in growing animals (From Kielanowski,1976)

Description and live weight of animals	N[2]	Method applied	Energy cost of protein deposition: Metabolisable energy[1] (kJ/g)	Energy cost of protein deposition: (Moles ATP/mole amino acid)	Reference
Milk-fed piglets, 2.5 to 8.5 kg	8	comparative slaughter	48.1 ± 1.97	32	Kielanowski and Kotarbinska (1970)
Milk-fed piglets, 4 ti 12 kg	60	comparative slaughter	50.8	36	Muller and Kirchgessner (1973)
Castrated male pigs, 20 to 40 kg	28	nutritional balance and direct calorimetry	41.2	23	Close, Verstegen and Mount (1973)
Castrated male pigs, 20 to 90 kg	48	respiration trials	54.9 ± 4.77	41	Thorbek (1970)
Castrated male pigs, 30 to 90 kg	54	comparative slaughter	66.8 ± 8.03	57	Kotarbinska (1969)
Castrated male pigs, 25 to 110 kg	4	respiration trials	45.6	29	Oslage, Gädeken and Fliegel (1970)
Castrated male pigs, 30 to 110 kg	16	respiration trials	44.1	27	Gädeken, Oslage and Fliegel (1973)

[1] The values are regression coefficients ± sample standard deviation

[2] Number of trials

Table 1.12 Metabolisable energy expended in protein deposition found from energy balance experiments (From Buttery and Boorman, 1976).

Animal	Energy cost (kJ/g) Protein	Source
Piglet	31.4	Kielanowski, (1965)
Growing Pig	46.2	Kotarbinska and Kielanowski, (1969)

The results determined by comparative slaughter tests seem to be more trustworthy than nutritional balance trials, in which nitrogen retention is often over-estimated, causing an underestimate of E.C.P.D. (Kielanowski, 1976). Comparative slaughter experiments show that the values of E.C.P.D. obtained with very young animals are lower than those obtained with older ones. This might be explained by the finding of Buraczewski and Pastuszewska (1974) that the proportion of amino nitrogen in total nitrogen in the body increases with age in rats and also in pigs (78 per cent at 10 and 89 per cent at 100 kg liveweight). It also seems probable that the fraction of free amino acids in the body decreases with advancing age proportionally to the relative diminution of body fluids. The same amount of nitrogen retained, therefore, would correspond to smaller amounts of true protein in younger than in older animals, and this might be reflected in the values of E.C.P.D.

The data in Tables 1.11 and 1.12 demonstrate that there is a definite relationship between the deposition of crude protein in the

tissues of growing animals and their energy expenditure (Kielanowski, 1976). Therefore, E.C.P.D. values are useful for the compilation of feeding standards.

Although estimates of E.C.P.D. can be regarded as true empirical indices, little can be said about their true physiological meaning. The energy cost of fat deposition in animal tissues, measured in respiration trials or estimated statistically, is consistent with the energy cost of fat synthesis, deduced from biochemical considerations (Armstrong, 1969). However, it has been deduced similarly that 8 to 10 moles of high-energy phosphate bonds are needed for the incorporation of one mole of amino acid into protein (Armstrong, 1969), an M.E. cost for synthesis of 1g protein of about 0.59 - 0.88 M.J. M.E. (Kielanowski, 1972a). This is considerably less than has been computed from the quoted values of E.C.P.D. (Kielanowski, 1976).

The processes of synthesis and breakdown are going on continuously in the organism. The net gain of protein in a growing animal should be regarded as a balance of these two processes (Millward and Garlick, 1972). Whittemore and Fawcett (1975; 1976) suggest that the total protein turnover is related to the rate of protein synthesis as well as total protein mass. The energy cost of protein turnover would therefore increase as lean body mass increases with time, and increase in animals with a higher rate of protein growth, e.g. boars, (Filmer and Curran, 1977).

1. Protein requirements for protein deposition

Although the calculation of protein requirement is complicated by protein recycling, an approximation can still be made. Lean growth contains about 22% protein (Whittemore and Elsley,1976). Losses from recycling are ∿6% protein cycled, decreasing from 13% to 6% of the

protein mass as the pig grows. Since protein mass is usually about 15% of liveweight, daily protein requirement at maintenance is 0.12 - 0.05% of body weight. The amount of protein necessary in the diet further depends upon the biological value of the protein and upon the amount digested (Whittemore and Elsley, 1976). The ARC (1967) recommendations are based on % of Dry Matter, and therefore depend upon the amount of feed. A more explicit manner of expressing requirement would be to give protein (in grams) requirements for pigs of various liveweights, since nutrient density of a diet (the concentration of nutrients and energy per unit weight of the diet) may be modified.

2. The rate of protein deposition

Where there are differences between pigs in final protein mass, the implications for growth will depend upon the presence or absence of a concomitant difference in the mature target for body protein in the mature animal. Thus where the mature target is similar, rate of protein growth will be less for pigs with lesser final protein (Fig. 1.13, case 2); conversely, a difference in mature age between pigs of similar mature mass has the unavoidable corollary that rate of protein growth is dependant upon age at maturity (Fig. 1.12, case 3). Should increased protein mass be also associated with an increase in age at maturity, then protein growth rate might be a relatively uncompromising factor, with age and mass dependant on it. It would appear likely in the case of the growing pig that the pertinent comparison is between cases 1 and 2 (Fig. 1.13); namely that pigs may have similar target mature ages and dissimilar mature masses with the result that a greater mature size is associated with a faster rate of growth. An increase in protein growth impulsion, however, probably

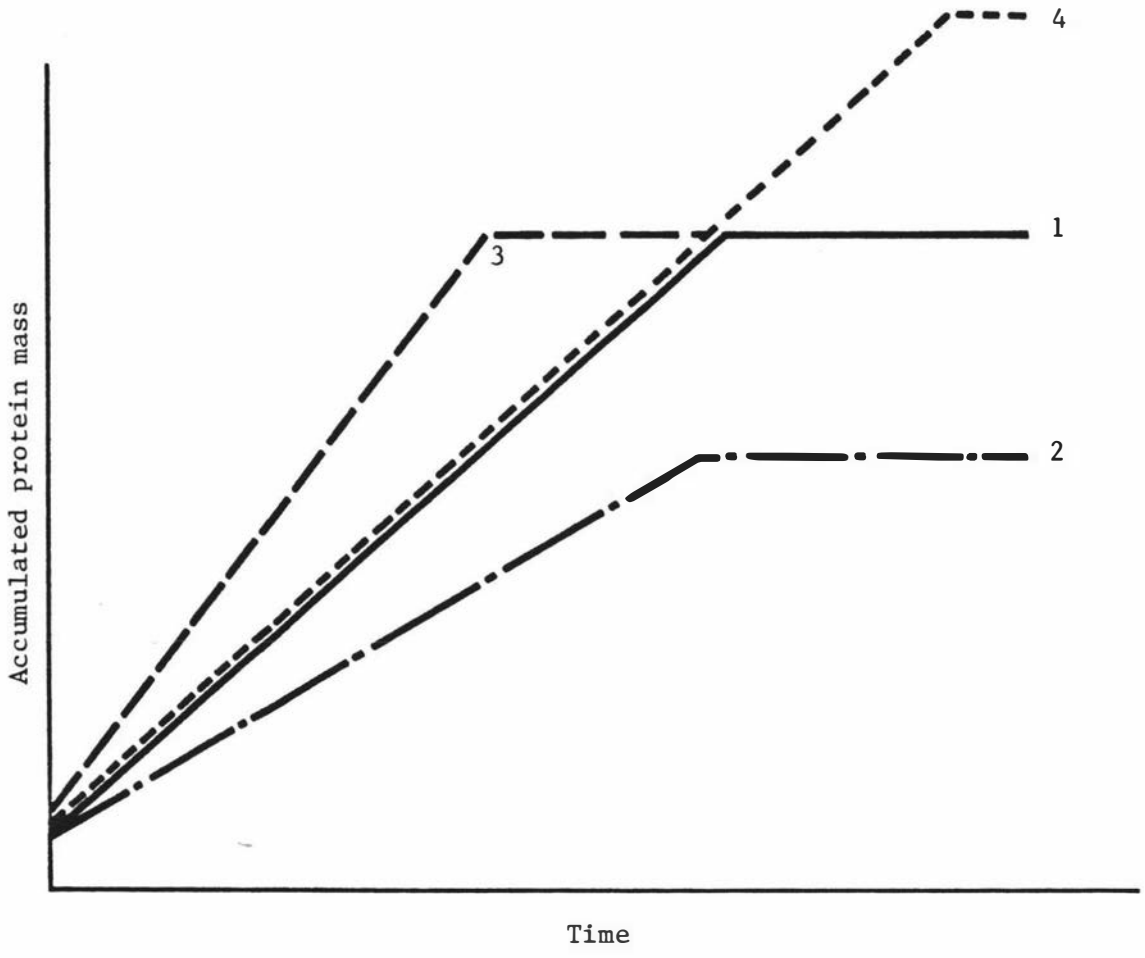


Figure 1.12 Rate of protein growth as related to mature protein mass. Using Case 1 as the datum. Case 2 is of similar mature age but of different mature protein mass, Case 3 is of different mature age but similar mature protein mass, Case 4 is of different mature age and of different mature protein mass but similar rate of protein growth (From Whittemore, 1977).

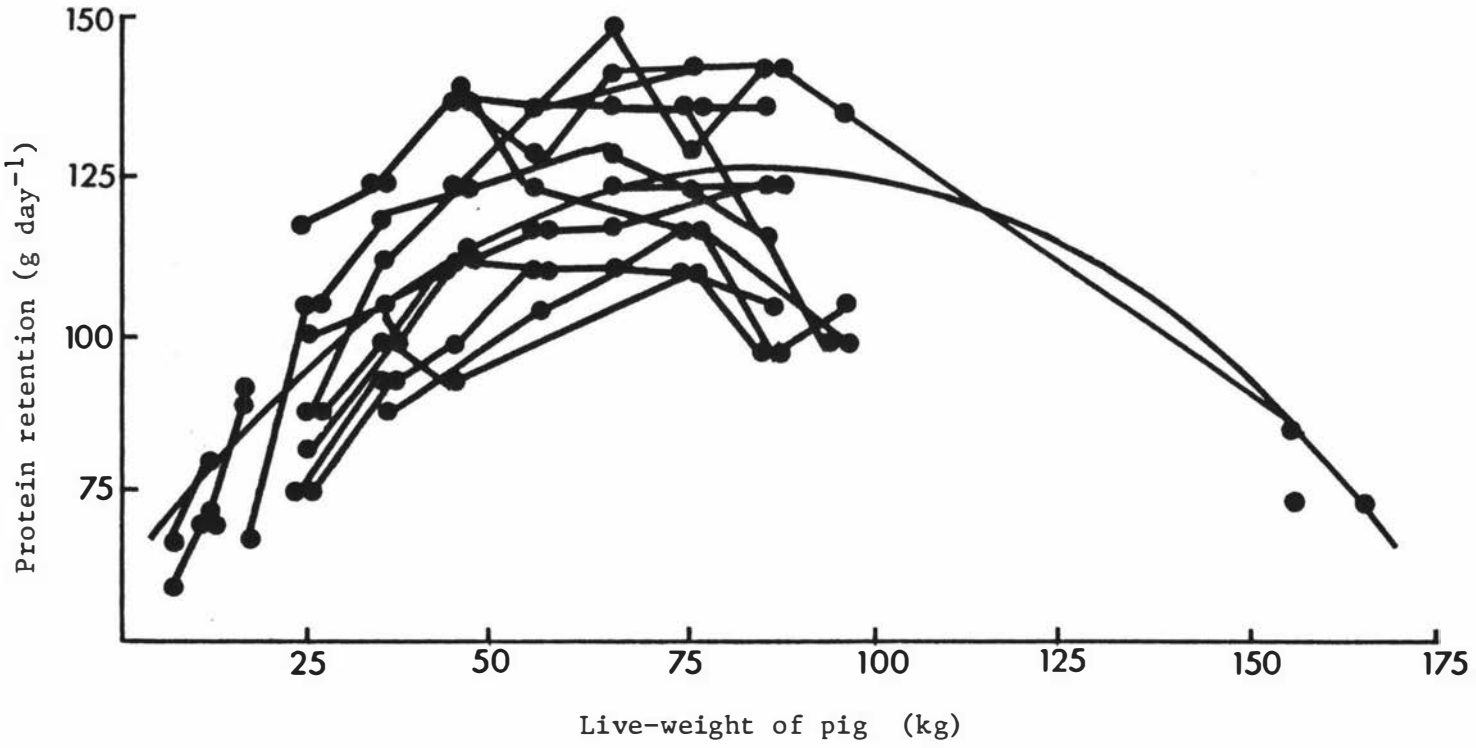


Figure 1.13 Daily protein retention in relation to live-weight (interpolated from data given by Thorbek, 1975). (From Whittemore, 1977).

will put back mature size to a certain extent.

Fig. 1.12 suggests that protein growth is linear, whereas convention demands a sigmoid curve. Analysis of 20 investigations of Thorbek (1975) confirms the relationship between protein retention (Pr) and liveweight (LW) may be quadratic (Fig. 1.13).

$$Pr = 1.63LW - 0.0094LW^2 + 60.$$

However, a possibility exists that the pig's potential for protein retention is not quadratic, but broadly constant over most of the growth phase (20-120 kg) and that failure to achieve the potential between 20 and 50 kg is resultant merely from inadequate nutrient supply (Whittemore, 1977).

1.5.5 Protein and energy interrelationships

The growth and body composition of pigs are influenced by both the composition and the daily intake of food (ARC, 1967). In particular, carcass leanness can be increased either by reducing the daily food intake, which also slows growth, or by increasing either the content or quality of protein in the diet, which within limits, increases growth rate. The availability of two simple means of varying carcass quality implies that, with any one prevailing set of feedingstuff and meat prices, there is an optimum combination of dietary composition and rate of feeding (Fuller et al, 1976).

Protein is required for the formation of tissues and enzymes, but may also be used as a source of energy in cases of energy shortage or excess protein availability. Estimates of maintenance requirement for protein derived from results of trials in which there was a loss of energy from body tissue are therefore of doubtful value (Van Es, 1972). Animals may also change to some extent their protein requirement

in cases of low and high protein supplies (Mollgaard, 1931; Paquay, 1968), due to a change in excretion of urea with the urine (Allison, 1959). The Nitrogen balance is clearly not a very sensitive indicator of sufficient supply of protein. The protein requirement is essentially a requirement for amino acids (Van Es, 1972). Differences in results between experiments (Chamberlain, 1972; ARC, 1967; Braude and Hosking, 1974; Chamberlain and Cooke, 1970; Davis et al, 1965; Robinson et al, 1964) are due to differences in the composition of cereal mixtures, breed of pig, feeding scale and method of feeding, physical environment, amino acid concentration in the protein and many other factors, which continue to make it difficult to regard the values quoted as anything more than a guide to the composition of practical rations. It is necessary to think in terms of differences in M.E. cost of maintenance and of unit (lg) protein deposition caused by different dietary protein levels.

The changes in performance that accompany changes in the plane of nutrition using a fixed diet can equally well be regarded as consequences of raised protein allowance as of energy intake, the two situations differing in that when protein percentage is increased there are only small changes in energy supply, when daily feed allowance is raised there is a proportional increase in daily energy (Chamberlain, 1972). Blair et al (1969a, 1969b) and Davies (1970) both agree that the rate of gain of lean meat responds to daily feed intake in pigs 25 kg liveweight fed ∿1 kg meal/day up to pigs 100 kg liveweight fed ∿3 kg which can be interpreted as a response to increased daily energy or protein allowance or both. The efficiency of utilization of protein for lean meat production declined as intake increased (Chamberlain, 1972).

It is well established that castrated males (barrows) produce fatter carcasses than gilts (Bowland and Berg, 1959; Charlette, 1961; Buck et al, 1962; Buck, 1963; Blair and English, 1963; Lidvall et al, 1964; Waldern, 1964; Bell, 1965; Lodge and Day, 1967; Bruner and Swiger, 1968; Hale et al, 1968; Young et al, 1968), referring to pigs fed to appetite or restricted within groups. Even where intake is controlled (Woodman et al, 1936; Lucas and Calder, 1956; Blair et al, 1969a; 1969b) gilts have been leaner than barrows. Recent work by Holmes et al (1980) has shown that nitrogen retention will increase in association with increases in nitrogen intake for all sexes at 30 kg liveweight, and for boars at 90 kg but not for gilts and barrows. Boars retained more nitrogen than barrows at 30 and 90 kg only if given the diet with the higher concentration of protein. This suggests that boars are more sensitive to dietary changes, and have a higher potential for lean gain. The figures for gilts suggest that they are less sensitive to dietary fluctuations with respect to energy or protein, and that their potential for rate of lean deposition is reached at a younger age than that of boars.

Timing of feed supply during the life of the pig might affect utilization. Andah (1970) concluded that use of a single protein level in diets would not affect the utilization of protein and energy. Yeo and Chamberlain (1966) and Frape et al (1968) report that cereal and supplementary protein components of a diet can be provided at separate daily feeds with no measurable effects on performance.

The Nodular Worm: *Oesophagostomum dentatum*

1.6.1 Introduction

It has long been recognized that helminths, present in sufficient numbers, can adversely affect their hosts. It was considered that, to a large extent, these adverse effects were directly attributable to the activities of the parasites - feeding on host tissues and blood, causing mechanical damage, interfering with digestive processes and competing for nutrients. This is a gross oversimplification of the situation and, in many respects, incorrect; the relationships of host and parasite are far more complex than had been imagined. For example, it was observed that heavily parasitized ruminants show a markedly reduced appetite and may not eat at all (Bennetts, 1933). A large body of scientific evidence has since accumulated to show that anorexia is indeed a common occurrence in most gastronintestinal nematode infections of ruminants (Spedding (1954), Gibson (1955), Horak and Clark (1964), Dobson (1967), McLeay *et al* (1973)). The mechanism by which anorexia is caused is unknown.

Hypoproteinaemia commonly occurs in nematode infections, but strictly speaking it is almost invariably a hypoalbuminaemia. Globulin levels are often raised above normal levels, presumably as a result of antigenic stimulation (Charleston, 1976). Work of Mulligan *et al* (1963) and Halliday *et al* (1968) suggested that the decrease in albumin levels might be due to leakage of protein into the gut lumen. Subsequent studies with many parasites have shown that a protein-losing gastroenteropathy is, in fact, usual in gastrointestinal nematode infections (Holmes and McLean, 1971; Bremner, 1969; Halliday et al, 1968). There is a growing body of evidence that

suggests that the protein loss is attributable at least in part to the host's immunological response to the parasite (Ogilvie and Jones, 1971). In experiments with sheep, Barger (1973) and Barger et al (1973) found evidence that those animals that most actively resisted larval challenge grew less wool, demonstrating that there is an energy cost in expressing resistance. Resistance to the establishment of a worm population should not be assumed to confer resistance to the metabolic effects of parasitism (Sykes, 1978).

Some parasites cause anaemia directly by blood removal (Soulsby, 1966), or indirectly through causing haemorrage into the gut or interference with erythrocyte production. The cause of the anaemia that commonly occurs in association with infections by gastrointestinal nematode parasites is largely a mystery (Charleston, 1976). There is evidence that gastrointestinal nematodes alter gut mobility and digesta flow in diarrhoeic sheep (Bueno et al, 1975; Ruckebusch, 1970). If prolonged, such changes could limit digestion, and may be a major contributor to body water loss.

Work with sheep (Sykes, 1978; Sykes et al, 1980; Sykes and Coop, 1976; Sykes et al, 1977) has shown that subclinical parasitism markedly reduces performance by exerting a wide range of effects on host physiology. Much of the detailed experimental work on the effects of gastrointestinal nematodes on the host relates to ruminants rather than monogastric animals.

1.6.2 Distribution of the genus Oesophagostomum

The genus Oesophagostomum is usually classified in the sub-family Oesophagostominae within the family Trichonematidae (Skrjabin et al, 1952) Cyathostomatidae (Yamaguti, 1959). The genus includes about

15 species which parasitise ruminants, pigs or primates. All mature in the colon of their respective definitive hosts.

Oesophagostomum radiatum, O. columbianum, O. venulosum, O. asperum, O. bhandari and O. multifoliatum are know from domesticated ruminants, but only the first three species are clearly of economic importance. Eight species of Oesophagostomum have been recorded from pigs (Table 1.13).

Table 1.13 Oesophagostomum species in the pig

Species	Reference
O. dentatum	Rudolphi, (1803)
O. brevicandum	Maplestone (1930)
O. georgianum	Schwartz and Alicata (1930)
O. maplestoni	Schwartz (1931)
O. quadrispinulatum (syn. O. longicandum)	Marconi (1901)
O. granatensis	Herrera (1958)
O. hsuingi	Ling (1959)
O. rousseloti	Diaoure (1964)

Oesophagostomum dentatum is one of the so-called "nodular worms" (see later section 1.6.5 for discussion), and is cosmopolitan in distribution wherever pigs are kept (Table 1.14). Though O. dentatum is the most common in occurrence, other species may occur in the same animal (Soulsby, 1965).

Table 1.14 Recorded cases of O. dentatum

Country where recorded	Example Reference
Australia	Dobson and Bremner (1974)
Belgium	Poelvoorde (1973)
Canada	Smith (1979)
Czechoslovakia	Dvorakova (1975)
Denmark	Jacobs (1966)
England	Goodey (1924a); Pattison (1976)
France	Graber, Raynaud and Euzeby (1970)
Germany	Nickel and Haupt (1969); Soller (1976)
Italy	Bellani and Cortelazzi (1973)
New Zealand	Whitten (1949); Ineson (1954)
Nigeria	Fabiyi (1979)
Poland	Tarczynski (1955)
Scotland	Jacobs and Dunn (1969)
South Africa	Horak (1978)
United States	Riddle et al (1972); Hass et al (1972)
U.S.S.R.	Kaarma (1974)

1.6.3 Prevalence of Oesophagostomes

The prevalence of infection with Oesophagostomum can be as high, or higher, in adult pigs than in younger ones, e.g. in adults 75-79 per cent (Boch and Neubrand, 1962), 96 per cent (Jacobs, 1965); in porkers 4-5 months old 64 per cent (Jacobs, 1965); in 2-3 month old weaned piglets 60 per cent (Boch and Neubrand, 1962).

According to Jacobs and Dunn (1969) Oesophagostomum is the most common helminth parasite of Scottish pigs, occurring in 67 per cent of porkers, 43 per cent of baconers and 94 per cent of the breeding stock, that is, most frequently and in the greatest numbers in the adult stock.

A slaughterhouse survey in Scotland over a two year period by Pattison (1976) showed the prevalence of O. dentatum infection to be 43 per cent in porkers, 33 per cent in baconers, and 85 per cent in sows.

In a study of 50 sows from 50 herds in East and West Flanders, 44 sows were found to be infected with O. dentatum, and about 75 per cent of all worms found were O. dentatum (Poelvoorde, 1978).

Riddle and Forrester (1972) describe the prevalence of helminths in swine in parts of South Carolina as: Oesophagostomum spp. 34 per cent, Ascaris suum 23 per cent, Strongyloides ransomi 7 per cent, Metastrongylus spp 6 per cent, Trichuris suis 5 per cent, Stephanurus dentatus 3 per cent.

Fabiyi from his study in Nigeria concluded that O. dentatum was common in all age groups, and that many pigs were infected with large numbers of the worms. Of pigs slaughtered for farmers at Pretoria Municipal Abbatoir, South Africa, 73 per cent were infected with parasitic helminths: 31 per cent with Ascaris suum, 65 per cent with Ascarops strongylina, 4 per cent with Metastrongylus apri, 27 per cent with Oesophagostomum spp, 15 per cent with Trichostrongylus colubriformis and 15 per cent with Trichuris suis (Fabiyi, 1979).

Young (1938) and Whitten (1949), cited by Ineson (1954), recorded the presence of O. dentatum in New Zealand. O. dentatum was recorded in 3 of 21 wild pigs examined (Ineson, 1954) but not in 25 domesticated pigs examined. Cairns and Hargreaves (1966) reported that O. dentatum commonly occurs in New Zealand; the "Veterinarian" (1968) refers to O. dentatum as being a nodular worm which is uncommon in New Zealand, or has little pathogenic effect. However, much of this information does not appear to be based on a large number of animals. There are

no reliable prevalence data for New Zealand.

It seems certain therefore that Oesophagostomum infection is of widespread occurrence in all classes of pig.

1.6.4 Identification and life cycle

Adult O.dentatum are 8-10mm long (male) and 11-14mm long (female) (Soulsby, 1965). Descriptions of this species are given by Goodey (1924a), Taffs (1966), Soulsby (1965), Lapage (1956) and Noble and Noble (1976). O. dentatum may be distinguished from the other common species in pigs according to the morphological differences given by Goodey (1924a; 1925) and Haupt (1966) between O. dentatum and O. quadrispinulatum, and from the descriptions of O. brevicaudum and O. georgianum given by Schwartz and Alicata (1930).

The life cycle patterns of individual species within the genus are similar. Infective third-stage larvae are found on pasture about one week after eggs are passed in faeces; the eggs are thin-shelled and strongylate in type. Larvae hatch after 24 hr at 22-24^{o}C, second-stage larvae develop in a further 24-48 hrs, and third-stage (infective) larvae develop in a further 48 hr. A third stage larvae may develop within five days under optimum conditions; infection is possible only by larval ingestion (Soulsby, 1965).

1.6.5 Pathogenesis and pathology of infection

McCracken and Ross (1970) studied the histopathology of O. dentatum infections in pigs between the ages of 3 and 6 weeks given single oral infections of 30,000 to 100,000 larvae. They found that lesions were first evident in the caecum 48 hours after infection, and consisted of focal thickenings of the mucosa up to 1mm in diameter. By day 4 numerous distinct nodules were present in the caecum and proximal and mid-colon. By day 6 the nodules had increased to 4mm in

diameter and were distinctly dome-shaped. The caecum and colon of pigs killed between days 7 and 10 after infection were contracted, with infolding of the mucosa. The caecum was commonly about half the length of that of uninfected pigs, and its wall was up to 3 times as thick. The larval nodules were at this stage approximately 8mm in diameter and had an umbilicated appearance due to a yellow or black central plug of necrotic material. Oedema was present in the wall of the caecum and colon. The contraction and oedema of the caecum and colon had disappeared by day 13. The nodules by this stage had lost their dark colour and gradually regressed so that no abnormalities due to larval infection could be seen in pigs more than 3 weeks after infection (McCracken and Ross, 1970). The site of larval penetration of the mucosa was marked histologically by connective tissue, leucocytes and giant cells. Where continuous infection took place, the colon particularly may be covered by a multitude of nodules, and large numbers of O. dentatum were found in the lumen. A general thickening of the wall of the large intestine and a catarrhal enteritis occured, which is associated with the clinical manifestation of diarrhoea. Ulceration of the mucosa may be evident, being due to both the adult worms and to the migration of the larvae into the lumen. The nodular formation may extend from the large intestine into the small intestine, particularly the terminal ileum (McCracken and Ross, 1970). Usually lesions are not found elsewhere, though enlargement of the mesenteric lymph nodules may be present. Because Oesophagostomum spp. commonly cause nodule formation in the mucosa, they are sometimes referred to as 'nodular worms'.

Jacobs (1967a) compared the linear distribution of two

Oesophagostomum species in the intestine of the pig. O.quadrispinulatum clearly favours a site closer to the ileocaecal valve than does O. dentatum. The territories occupied by each species were, however, observed to overlap to varying degrees, O. quadrispinulatum sometimes extending into a more distal site, and O. dentatum sometimes taking a proximal position. Attempts to correlate these variations with:

1) the absolute magnitude of the Oesophagostomum populations;
2) the relative numbers of each Oesophagostomum species;
3) the presence or absence of Trichuris suis;
4) the reproductive status of the sow;

failed to show a consistent pattern. Predictably, males and females of each species occupied similar positions in the intestine. Pairs of Oesophagostomum were often found in copula, and in each case mating involved males and females of the same species. Measurement of over 2,000 Oesophagostomum spp. individuals did not reveal any significant difference in the lengths of the worms taken from each section of the large intestine, nor did microscopical examination show any morphological differences which might indicate a progressively older population in the more distal segments (Jacobs, 1967a).

1.6.6 Transmission

Pastures contaminated with developmental stages of the Oesophagostomum species of swine can remain infective from one year to the next. In a field experiment in Germany, infective larvae of O. dentatum and O. quadrispinulatum contained in porcine faeces were placed on a pasture in September and October. Some larvae survived the winter period from October to mid-April. These larvae were shown to be infective for pigs (Haupt, 1969). Barnett (1966) studied the post-parturient rise of faecal nematode egg counts in sows. Mean

egg counts were related to the reproductive cycle, and showed a peak at six to eight weeks after parturition. Support for the role of the sow in transmission of Oesophagostomum infections to piglets is also given by Dvorakova (1975) and Jacobs and Andreassen (1967).

By nature the pig is an omnivore adapted to rooting and grazing, but domestication has largely overriden nature and the pig is usually housed with little or no access to pasture. Faeces from infected animals could therefore become highly concentrated, and where a large number of infective larvae develop, a situation where animals could become heavily infected may arise. Pigs, when kept in pens, will habitually defaecate in one particular area rather than at random. Thorough cleaning to remove all infective material should result in a severe reduction in numbers of available eggs and larvae (Pattison, 1976).

Henle (1975) studied the viability of helminth eggs in liquid pig manure. In laboratory experiments the percentage survival of eggs of Oesophagostomum from pigs decreased with increasing duration of storage in fermented pig manure. Summer storage killed all eggs within 12 days, whereas the winter storage period required was at least 30-50 days. Burden and Ginnivan (1978) studied the destruction of pig helminth ova and larvae in a slurry treatment process. Pig slurry diluted with water to about 4.5 per cent total solids was aerobically fermented in a 15 litre digester maintained at 55^{o}C. The contents were stirred at 100 rpm. The average treatment time was 4 days. Over 99 per cent of Oesophagostomum eggs and larvae were killed after half an hour. However, Soller (1976) examined the effects of various activated sludge plants on the development capacity of thin-shelled nematode eggs. He concluded that none of the activated sludge plants studied had a significant damaging effect on the eggs,

and that livestock waste-water clarification installations do not provide an environment conducive to destruction of parasite eggs.

Some evidence exists that transmission of nematode infective larvae by Psychoda flies (Bovien, 1937; Jacobs et al,1968; Tod et al, 1971) by rats (Jacobs et al, 1968) and by earthworms and cockroaches (El Rafail, 1963) is possible. However, it is probable that such means are of very lttle real significance in the field.

No study of the epidemiology of Oesophagostomum infections of pigs in New Zealand has been carried out.

1.6.7 Effects on pig health and production

The development of an aquired resistance to helminth parasites is the rule rather than the exception. The degree of resistance shown is relative, rarely absolute, and is dependant on a variety of host and parasite factors. Generally the more intimate the contact between the parasite and host tissue, the greater the resistance elicited. Resistance wanes without further antigenic stimulation, so that relatively frequent invasion of the host is necessary if the resistance is to be maintained (Taffs, 1966).

With Oesophagostomum, Nickel and Haupt (1964) found that the course of events after infections with 8,000 larvae was the same in piglets aged two to three months, which had not been exposed to infection before, as it was in pigs 8 months old which had been repeatedly reinfected. From these experiments they concluded that the nodular worm did not evoke the development of effective resistance.

Nematodes of the genus Oesophagostomum commonly occur in pigs but comparatively little is known of their effects on pig production. Some aspects of this were investigated by Shorb (1948), who observed anorexia, constipation, sometimes diarrhoea and emaciation, terminating

in death in severely affected animals. Davidson and Taffs (1965) have shown that looseness of faeces or diarrhoea, or faeces containing specks of blood and mucus can be produced in SPF pigs infected with Oesophagostomum larvae. Three out of four pigs showed anorexia, and two out of four lost weight. Some of these signs appeared as early as the fourth day after infection. Increases in body temperature were not observed and infections with 5,000 larvae caused no clinical signs. Nickel and Haupt (1964) obtained similar results, except that diarrhoea was not apparent, even in heavily infected, newly-weaned piglets.

In heavy natural infections, one or more of the above signs may or may not be apparent; the faeces usually appear normal (Taffs, 1966).

More recently Kaarma (1974) infected six parasite-free piglets with 10^5 Oesophagostomum dentatum larvae, leaving six other piglets as controls. Symptoms of illness were most severe in infected piglets during the first 10 days after infection. Liveweight gain by the infected pigs during this period was 15 per cent and 45 per cent of that of control pigs in the first and second trials respectively. Infected piglets had capricious appetites; their feed consumption was lower, the apparent digestibility of organic matter and the assimulation of digested nitrogen decreased in comparison with control-group piglets.

In a series of three experiments, pigs weighing 35-37 kg were given a unrestricted ration either low in protein (12.3 per cent Digestible Crude Protein) or with a normal protein concentration (16 per cent DCP). In pigs dosed with 10^4 O. dentatum larvae once weekly for six weeks, erythrocyte count and weight gain were lower in the infected, low protein pigs than in the others (Poelvoorde and

Berghen, 1978). In pigs 35kg liveweight, and dosed with 6.4×10^5 O. dentatum larvae over 8 weeks, plasma sodium concentration became subnormal from the third week of infection in infected pigs; plasma potassium was not affected compared with controls (Poelvoorde and Berghen, 1979a). In pigs 32kg liveweight which received a single dose of 5×10^4 O. dentatum larvae, no difference in body weight or food consumption existed between control and infected pigs (Poelvoorde and Berghen, 1979b). The differences between the results of these experiments may indicate that heavy natural infections (simulated by the first and second experiments) may be more damaging to productivity than a single infection in pigs of this liveweight.

The results of Hass et al (1972) are in conflict with the results of Poelvoorde and Berghen, (1978; 1979b) cited earlier. Hass et al (1972) dosed pigs 7-8 weeks old with one or several doses of infective Oesophagostomum larvae and killed the pigs seven weeks later. A single dose of 5×10^3 or 3×10^4 larvae adversely affected weight gain and resulted in moderately large parasite populations. Repeated daily doses of 250, 750 or 1500 larvae given on 5 days each week had a less adverse effect on weight gain, although the established parasite populations were equal to or greater than those resulting from larger single doses. An initial dose of 5×10^3 larvae followed by 250 larvae daily reduced weight gain and resulted in establishment of the largest parasite populations. Hass concluded from these data and those of previously published reports, that there seems to be no single factor which accounts for the variable adult nodular worm counts obtained from pigs given experimental infections (Hass et al,1972).

Contradictions to the above findings were noted by Pattison et al. (1980) who report that pigs have tolerated, with no adverse effect on

health, larval levels of up to 2×10^4 (Nickel and Haupt, 1964), 3×10^4 (Jacobs, 1969) and 10^4 (McCracken and Ross, 1970).

Complications from bacterial infections may occur. Massive experimental infection of young pigs with 20-190,000 infective O. dentatum larvae resulted in activation of facultative pathogenic bacteria (Salmonella cholerae-suis) in the intestine, and produced clinical symptoms and lesions of a paratyphoid infection (Kotlan, 1956).

The effects of subclinical nematode parasitism on reproductive performance in the sow, and on digestion and performance in growing pigs was studied by Pattison, Smith and Thomas (1979) and Pattison, Thomas and Smith (1980). Successive doses per sow of 2×10^5 larvae at mating and 10^4 larvae 10 weeks later affected subsequent performance in comparison with control animals. Infected sows averaged 12.4 pigs born, of which 9.5 were born alive; worm-free sows average 12.8 pigs born, of which 11.3 were born alive. Worm infection reduced birth weights by 15 per cent but differences were statistically non-significant. Litters were equalized at eight pigs shortly after birth, and subsequent weaning weights at 35 days were 10.5 per cent lower for piglets from infected sows despite a 29 per cent higher consumption of creep feed. Clinical disease was never observed in the infected sows, and no parasitic infection was found in the piglets (Pattison, Smith and Thomas, 1979).

Growing pigs infected with O. dentatum in doses of 2×10^4, 4×10^4, 8×10^4 or 10^5 larvae reduced growth rate by 3, 8, 18 or 13 per cent respectively and increased feed conversion ratio by 15% in the 10^5 larvae treatment, compared with controls. For the 10^5 treatment, there was no effect on killing-out percentage or area of

of eye muscle in cross-section, but infected pigs had relatively lower backfat depths (5.5 to 12.5 per cent). Infection did not influence nitrogen retention, but apparent digestibility of the dry matter, organic matter, nitrogen, gross energy and crude fibre was reduced (Pattison, Thomas and Smith, 1980).

In comparing reports, problems arise due to the variability of larval doses, age and breed of pig, and diet. The parameters measured also vary, and may partly reflect variations in experimental design, procedures and differences in strain of parasite.

1.6.8 Diagnosis and control

Diagnosis is based on clinical signs which, however, may not be specifically characteristic, and on diagnostic procedures, for example, the examination of faeces for worm eggs and by the demonstration of lesions and parasites at post-mortem examination. A diagnostic problem must be of deciding how to interpret a particular worm burden,given the conflicting experimental data.

Diagnosis is often made more difficult by the presence of simultaneous infections by other organisms. Little is known about the inter-relationship of bacteria, virus and nematodes, particularly the association of bacteria with the gut nematodes, but evidence suggests that much more research should be done on this. For instance, massive infections with Oesophagostomum may provoke an acute or chronic salmonellosis with a typical post-mortem picture of piglet paratyphoid (Kotlan, 1956; Nickel and Haupt, 1964). Taffs, Sellers, Clark and Froyd (1969) compared Oesophagostomum faecal egg counts with post-mortem worm counts in 68 naturally-infected pigs. Faecal egg counts may be influenced by various host and parasite

factors, but Taffs et al (1969) observations indicate that in growing pigs there is a direct linear relationship between faecal egg counts and total number of worms. However, the wide scatter of actual worm numbers for animals with similar egg counts emphasises the inaccuracy that could arise from reliance on egg counting alone. No statistical inferences were taken from the data.

Under field conditions pigs are often infected simultaneously with several different helminths, commonly with the trichostrongylid nematode Hyostrongylus rubidus. It is difficult to differentiate between Oesophagostomum and Hyostrongylus infection by examination of eggs from faeces, as both are typically ovoid and thin-shelled, although they differ slightly in width. Hyostrongylus eggs measure from between 31 to 40 µm (Skrjabin and Bekenskii, 1925; Alicata, 1935; White, 1955), whereas eggs of Oesophagostomum vary in width from 38 - 53 µm (Alicata, 1935). Hyostrongylus eggs are generally passed in the 32 cell or early tadpole stage, whereas Oesophagostomum eggs are often passed in the 8 to 16 cell (early cleavage) stage (Alicata, 1935). Such a distinction could only be made for eggs examined immediately after being passed. However, despite these differences, the best method of differentiation is by faecal culture and the examination of third-stage larvae for size and morphology of the sheath. H. rubidus larvae are much longer and thinner (length and width with sheath is 800 by 20 µm, Goodey (1924b); without sheath is 715 to 735 by 22 µm, Alicata (1935)) than are O. dentatum larvae (length and width with sheath is 660 to 720 by 30 µm, Goodey (1924a), 560 to 600 by 28 to 30 µm, Kotlan (1948); without sheath is 500 to 532 by 26 µm, Alicata (1935)). The extension of the sheath beyond the tail of the larva is short in H. rubidus but long and whip-like

in Oesophagostomum spp.

Control in permanently housed animals should be easy if standards of hygiene are high and pens are kept as dry as possible (Taffs, 1966). Oesophagostomum larvae take at least five days to reach the infective stage, and require moisture (Pattison, 1976).

Where animals are kept for all or part of the time on pasture or deep litter, control by prevention of infection is more difficult and absolute control is impossible. In such cases control may rely on the use of anthelmintics or combinations of mangement procedures and dosing, eg. sows before farrowing, young pigs before weaning (Thomas and Smith, 1968; Taffs, 1966).

Many anthelmintics have been tested against Oesophagostomum in pigs (Table 1.15).

young pigs	Destomycin	10g/ton in feed	worm eggs	eliminated after 60 days	Liberge (1973
	Dichlorvos Dichlorvos	V22 formula V13 formula	15 & 25 days 15 & 25 days	highly effective	Hass (1975)
	Cambendazole oral	15mg/kg Bwt 20mg/kg Bwt 25mg/kg Bwt	10 day larvae	not effective	Taffs (1976)
adult & growing	Thiophanate	50mg/kg		96-99%	Baines et al (1976)
growing and breeding	Fenbendazole	15ppm for 6 days		Effective control	Enigk et al, (1977)
	Oxfendazole	3mg/kg		reduced/ eliminated egg prod^{n} & intest. population	Corwin (1977)
	Levamisole hydrochloride	7.5mg/kg	adult immature larval	79-96% 84-99% 65-92%	Oakley (1977)
	Febantel	5mg/kg	7 days post-inf. 14 days post-inf. 28 days post-inf.	97.5% 99.5% 99.7%	Connan (1978)
	Rintal (Febantel)	5mg/kg 10mg/kg 15ppm for 3 days	8 day larvae 18 & 45 day larvae all stages adults only	95% 100% 100% 100%	Enigk and Dey-Hazra (1978)
Brdg sows Growing	Thiophanate	0.045% ration 0.025% ration (14 days)		decreased egg hatchability to nil	Baines et al.(1979)
Sow	Dichlorvos	4mg/kg Bwt/day		11% improvement reproductive efficiency	Young et al. (1979)

CHAPTER TWO

MATERIALS AND METHODS

Experiment 1: Energy and Nitrogen Metabolism Study

2.1 Plan of Experiment

The major objective of this experiment was to determine the effect of Oesophagostomum dentatum infection on the energy and nitrogen metabolism of the growing pig.

Two groups, each of four pigs, were selected and allocated to four treatments, each replicated once. The plan of the experiment was:

2 infection treatments	x	2 planes of nutrition
(Infected, Uninfected)		(High, Low)

This was designed to determine whether level of feeding influenced the establishment of a worm burden, and whether energy and nitrogen metabolism changed in response to the burden. The experiment was a split-plot design.

2.2 Animals

Four Landrace x Large White gilts from each of two litters were selected from the Massey University Pig Herd. The pigs within each group were chosen to be similar in liveweight, and they were then randomly allocated to treatments.

The first group (replicate) was taken in November, 1979, and the second in January, 1980, - 54 days apart. After being weaned at 5 weeks, these pigs were moved to individual pens at the Massey University's Animal Physiology Unit when they weighed about 18 kg.

2.3 Preparation of Larval Cultures and Infection of Pigs

The digestive tracts of five sows were collected from the pig killing floor of the Kiwi Bacon Company, Longburn, Palmerston North. Sows were chosen rather than growing pigs because these were more likely to yield Oesophagostomum dentatum (Pattison, Smith and Thomas, 1979). The large intestine was cut open, washed over a 22 mesh sieve, and worms of one tract were collected from the mucosa between the caecum and anus. Samples of faeces were collected to be examined for worm eggs. Samples of worms were identified (with the help of Dr. W.A.G. Charleston, of the Department of Veterinary Pathology and Public Health, Massey University) using the methods of Soulsby (1965; 1969). Examination of approximately 50 worms indicated all were O. dentatum. Subsequent work with the isolate indicated that there was a small proportion (estimated to be 1-2%) of O. quadrispinulatum present. The worms were washed and put into saline for storage, subsequently ground with washed sand, and added to equal volumes of autoclaved pig faeces and vermiculite. The culture medium was put into Agee jars, half-filling each one, so that an airspace was left at the top. The jars were covered with loosely fitting lids and stored at 27°C for 7 days; a fine spray of water was added when necessary to keep the medium moist.

When ready for harvest, the larvae could be seen ascending the side of the jar. They were recovered initially by rinsing from the sides of the jar once daily. After about five days, the recovery was done using the Baermann apparatus (Baermann, 1917. Anon, 1971) as described by the Ministry of Ag. Fish. and Food (1971) (Figs. 2.1 and 2.2). Examination of several hundred larvae showed that all were Oesophagostomum larvae rather than Hyostronglus larvae (Fig. 2.3).

Figure 2.1 O.dentatum culture medium and harvested larvae

Figure 2.2

Baermann technique for harvesting larvae

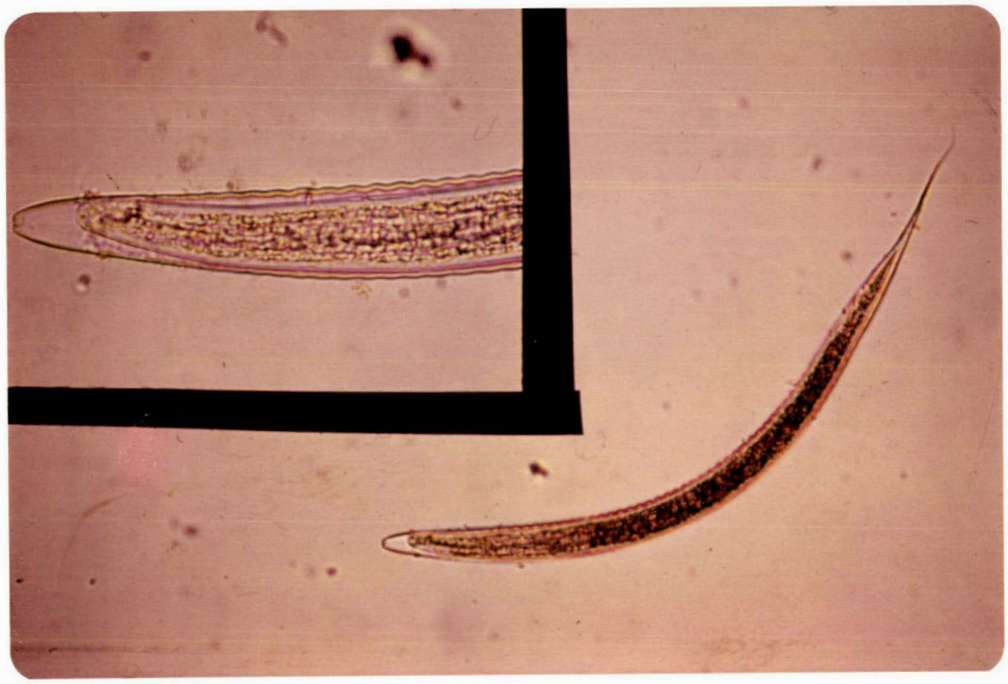


Figure 2.3 Infective third-stage larvae from cultures of O.dentatum used for infecting pigs. (magnification 250 x and 100 x)

The larvae were then pooled into a 'pure' culture and a previously worm-free 'donor' pig was dosed. After 21 days the infection was patent (i.e. eggs began to appear in the faeces). The faeces from this animal were then used as a source of further worm eggs which were cultured as described above. The larvae harvested from this culture were also examined for presence of Hyostrongylus. None were found.

The larvae were collected, counted, and doses of 80,000 larvae in water were prepared for adminstration to those pigs which had been allocated to the infected treatment.

All pigs were treated with an anthelmintic preparation, levamisole, as recommended by the manufacturers (Nilverm, ICI Tasman Ltd., N.Z.) after they were moved to the Physiology Unit. Infected treatment pigs were later dosed at about 20kg liveweight with 80,000 Oesophagostomum dentatum larvae in water. This was done by two persons, one restrained the animal in an upright position, while the other after inserting a gag, tipped the dose down the pig's throat. The dose was rinsed down with distilled water.

2.4 Housing

The animals were placed in 1.0m x 1.7m individual pens in a 6.0 x 4.5m room at the Animal Physiology Unit. Six pens were arranged either side of a common aisle, with all doors facing into this aisle. The pens had previously been scrubbed and sprinkled with sodium hypochlorite. Infected pigs were kept strictly to one side of the aisle, and uninfected pigs to the other, in an effort to avoid cross-infection. Where possible, pigs were kept in the same pen when not in the calorimeter. Galvanized iron footbaths which extended across the opening of a gate were filled with a 3% chlorine solution and placed

outside the uninfected animal's pens.

2.5 Feeding and Management of the Pigs

Two pigs per replicate were randomly allocated to a plane of nutrition (H) corresponding to 90% of appetite; this plane of nutrition increased from 1.22 kg/day at 20 kg liveweight to 2.88 kg/day at 80 kg liveweight (see Appendix 2). The remaining two pigs were allocated to a plane of nutrition (L) corresponding to 57% of appetite; this plane of nutrition increased from 0.76 kg/day at 20 kg liveweight to 1.82 kg/day at 80 kg liveweight. These levels of appetite were determined for use in a previous study (Holmes et al, 1979). Water was available ad libitum.

Feed was provided by the Massey Piggery and was the unit's commercial grower ration. The percentage composition and calculated nutrient content are given in Appendix 1.

Pigs were weighed at 0800 hours once weekly, before being fed; these weights were used to calculate the amounts of feed to be allocated to each pig during the next 7 days (see Scale of feeding, Appendix 2).

Pigs which were about to undergo a balance period were changed to their new feed allowance two days before the balance began. A sample of feed was taken each week, and stored for later analysis for dry matter, nitrogen and energy concentrations.

2.6 Allocation to Calorimeters

Pigs were assigned to either of the two calorimeters randomly at their first balance; in a subsequent balance, those pigs occupied alternate calorimeters. Successive treatments within each calorimeter changed with each balance.

For example:

		Cal 1	Cal 2
Balance	1	IH	NH
	2	NL	IL
	3	NH	IH
	4	IL	NL
	5	IH	NH
	6	NL	IL

All animals were subject to a five-day training period in the calorimeters before taking measurements. There were two calorimeters capable of housing an animal each, so infecting of the 'H' and 'L' pigs was performed in alternate weeks. For each replicate, the first two pigs to have balances performed were 'H' animals. A balance was of seven days duration (Table 2.1). The calorimeters were scrubbed and disinfected with a 2.25% strength chlorine solution at the conclusion of each balance. The two 'L' animals followed in the subsequent week. Two balances in alternate weeks were performed per pair of pigs, then there was a gap of two weeks, followed by the last balance per pair of pigs (Table 2.1).

2.7 Calorimetry and Balance Method

2.7.1 The open-circuit respiration calorimeters

The calorimeters used in this study have been described by Holmes (1973). Each consisted of a chamber of galvanized steel on a rigid steel framework, 1.7m x 0.7m x 1.5m high (internal measurements), and a front and back door which sealed on to rubber gaskets. A food and a water trough were mounted on the front door, accessible through a lid, 0.3m x 0.3m, which also sealed on to a rubber gasket. The floor of each chamber was in the shape of a funnel, for urine drainage. Entry of air through the urine drainage tube was prevented by a 'liquid trap'. The animals were supported above the

Table 2.1 Sequence of events for calorimetry trial

Similar programme for both replicates

Age of H.P. Animals	High-Plane Animals	Low-Plane Animals	Age of L.P. Animals
5 wks	Selection at 18 kg and anthelmintic treatment Training in calorimeters	Selection at 18 kg and anthemintic treatment	5 wks
6 wks	Infected treatment animals dosed with O. dentatum at 20kg LWt	Training in calorimeters	6 wks
7 wks	First balance period	Infected treatment animals dosed with O. dentatum at 20kg LWt	7 wks
8 wks	7 days in pen	First balance period	8 wks
9 wks	Second balance period	7 days in pen	9 wks
10 wks	7 days in pen	Second balance period	10 wks
11 wks	7 days in pen	7 days in pen	11 wks
12 wks	7 days in pen	7 days in pen	12 wks
13 wks	Third balance period	7 days in pen	13 wks
14 wks	Removed to piggery, to grow to 80 kg	Third balance period	14 wks
		Removed to piggery, to grow to 80 kg	15 wks

floor of the chamber on aluminium slats. The calculated volume of each calorimeter was 2,200 litres. The air temperature within the calorimeter was controlled at 20°C (± 2°C) by means of a water-cooled, fan ventilated heat exchanger and thermostatically controlled electric heaters mounted above a false ceiling beneath the top of each chamber. A hygrometer and a thermometer set in the calorimeter wall could be read from outside. Each chamber was insulated externally with expanded air polystyrene, 2.5cm thick.

Air was exhausted from each chamber by a rotary pump, and fresh air drawn in from a height of 5m above ground level outside the building. Both chambers operated at a pressure which was approximately 2cm water gauge below atmospheric pressure, and were located in a well ventilated, temperature-controlled room. The exhaust air from each chamber passed through a device which cooled it to about 3°C; the air was assumed to be saturated with water vapour at this point. The air was rewarmed to 28°C, and drawn through two dry gas meters in series. The air temperature was measured as it left the cooling device and again as it left the gas meters. Estimates of water vapour pressure together with barometric pressure readings made it possible to correct the measured volume of air to standard temperature and pressure.

An automatic solenoid switching system enabled small samples of air (1 litre/min) to be drawn by a small electric diaphragm pump from both the incoming fresh air entering the exhaust air leaving the chambers. These samples were dried by being drawn through silica gel. The system of solenoid valves allowed air to be drawn from the exhaust from each chamber alternately for four minute periods, and from the incoming fresh air for six minute periods, every four hours. Samples were also drawn into three glass cylinders, fitted with mercury-O-ring

sealed piston spirometers; one for exhaust air from each calorimeter, and another from air in the room, over a twenty-one to twenty-three hour period.

The first samples described were pumped through an automatic infra-red carbon dioxide analyser (Grubb-Parson, UK; range 0-1.5% CO_2) and an automatic paramagnetic oxygen analyser (Servomex Co. Ltd., UK; range 19-21% O_2) connected in series. The electrical output of each analyser was connected to one channel of a two channel recorder (Honeywell, UK; 5mV full scale). The recorded traces for the period could be integrated with a travelling planimeter. The second samples described were passed through the analysers in turn until the recorder trace became steady.

The gas analysers and the recorder were calibrated daily by pumping through them two compressed gas mixtures containing known concentrations of oxygen, carbon dioxide and nitrogen. The oxygen and carbon dioxide content of these gases were 19.031% O_2, 0.710% CO_2 and 20.198% O_2 and 1.279% CO_2 respectively. The calculated respired gas volumes, corrected to STP were further adjusted for the change in the chamber air composition between the beginning and end of each measurement period.

Heat production was calculated from the equation of Brouwer (1965):

$$HP = (O_2 \times 16.18) + (CO_2 \times 5.02) - (N \times 5.99)$$

where HP = heat produced (kilojoules kJ/24 hr)

O_2 = oxygen consumed (litres/24 hr, STP)

CO_2 = carbon dioxide produced (litres/24 hr, STP)

N_2 = urinary nitrogen excreted (grams/24 hr).

See appendix for worked example of Heat Production.

2.7.2 Tests of the calorimeters

A test of the whole calorimetric system comprising the chamber, ventilation circuit, dry gas meter, gas analysers, recorder and calibration gases, was to admit dry nitrogen or dry carbon dioxide gas into the calorimeter chamber at a measured rate, and to use the calorimetric equipment to estimate the gas admission rate. In a series of five tests, the measurement of oxygen averaged 0.99 accuracy, and in a further series of two tests, averaged 0.996 accuracy.

The whole apparatus can also be tested by the controlled burning of a weighed amount of absolute alcohol within the calorimeter. In this case, there is a change in composition of gases between entering and leaving the system due to the combustion of alcohol, corresponding to the effect an animal might produce if it were enclosed in the calorimeter. For these tests, the amount of CO_2 produced is calculable, providing there is complete ignition of the alcohol. A series of such tests produced a mean measured value of 97.1% ($\pm$ 0.7%) of the theoretical oxygen consumption.

2.8 Collection of Faeces and Urine

The animals confined in the calorimeter were supported on aluminium slats above a floor which sloped to an outlet near the front. Urine was collected through a pipe into a plastic bucket beneath the calorimeter. The urine was collected over 100 mls 0.1N H_2SO_4, strained through a sieve daily and bulked for the seven day balance period. The accumulating urine was kept in plastic buckets and stored at 4^oC until the end of the balance period. It was then weighed, thoroughly mixed and sampled. Later, determinations were made for nitrogen and energy.

Faeces were collected during the balance period from the slatted floor and from a removable polythene sheet beneath. A sample of faeces was collected each day, placed in a plastic screw-top jar and taken to the laboratory for egg counts. The weight of this sample was recorded and added to total bulk faeces for the week. Faeces were bulked over the 7 day balance period and stored at $-3^{o}C$. It was then weighed, mixed and sampled for determinations of dry matter, nitrogen and energy.

Refusals and spillages were collected at the end of each balance period for pigs undergoing balances. These were analysed for dry matter.

2.9 Analytical Techniques

Chemical analyses were done in duplicate with agreement between duplicates 3% or better, with the exception of gross energy determinations for urine. Repeatability for urine was accepted with duplicates of 10% or better.

Dry matter. Faeces bulked over the seven day balance period were thoroughly mixed on a clean concrete floor by shovel, and sampled. Duplicate trays of 300g faecal matter were oven dried at $80^{o}C$ for dry matter determinations.

Nitrogen. The nitrogen concentrations of feed and excreta were determined by the macro-kjeldahl method, described by AOAC (1965).

For meal about 1g of ground and mixed meal was weighed into a small plastic bag which had zero nitrogen content, and digested in flasks. The digesta was refluxed with Sodium Hydroxide, and was collected by being distilled in boric acid, and titrated back with 0.1M H_2SO_4.

A sample of the ground and mixed meal was oven dried simultaneously.

For faecal material a 300g freeze dried sample was ground finely, subsampled and a macro-kjeldahl determination performed as described (above) for meal.

For urine a weighed 10g wet sample of urine was pipetted into a small plastic bag, and a macro-kjeldahl determination made as described above.

Energy. Gross Energy content of meal, faeces and urine were determined by an Adiabatic Bomb Calorimeter (Gallenkamp & Co., UK.).

Ground and mixed meal powder, prepared as above, was measured into a pelletizing clamp, and pellets of 1.0g formed for combustion. The pellets were weighed, placed in the combustion chamber of the bomb calorimeter and O_2 admitted under pressure. The combustion chamber was placed in a bucket of water containing a weighed amount of water, and this in turn was placed in the Bomb Calorimeter which had a circulating water jacket surround and an insulated lid. The temperature of the water was noted, the sample was ignited, and the temperature noted again after it had stabilized.

Ground and mixed faeces samples were treated in the same way as described for meal powder Gross Energy determinations above.

Urine samples were prepared by pipetting 50g (mls) on to a weighed polythene (Gladwrap) film supported in a petri dish, and frozen. The samples were then placed in a freeze dryer, and once dried, the polythene and sample were combusted together in a similar manner as that for meal and faeces described above. Corrections were made for the energy content of the polythene.

2.10 Exsheathment Work with O.dentatum

The larval suspensions which were kept to be used later for dosing the experimental pigs appeared to have a reduced activity. This led to an attempt to find a means of exsheathment so that larval vaiability could be assessed, since none were found in the literature. Buffers were produced by combining citric (0.1M) and Na_2HPO_4 (0.2M McIlvaine's solution), to form six 10 ml aliquots, ranging in a step-wise fashion from pH 8.0 to pH 3.3. Equal amounts of larvae were added to each solution and also to a 10 ml distilled water blank. Carbon dioxide was bubbled through each solution for 5 minutes. The jars were capped tightly and put in a water bath at $39^{o}C$ for 3 hours. A second 10 ml distilled water blank was prepared with the same concentration of larvae as the incubated samples. This sample of larvae was killed by plunging the jar into boiling water without buffer or incubation, but with carbon dioxide treatment, and the percentage exsheathment was estimated. The incubated jars were removed, plunged in a boiling water bath for one minute to kill the larvae, and each solution then inspected for proportion of sheathed and exsheathed larvae using a counting grid.

2.11 Faecal Egg Counts

Throughout the trial faecal samples were collected daily for the duration of the balances, whether the pigs were in or out of the calorimeters (so that egg counts could be measured in the infected and uninfected pigs). Dung samples were taken from four or five different places in a pen, in an attempt to achieve representative sampling, and examined in the laboratory for the presence of eggs using

a Modified McMaster method.

Where storage of a sample was required (usually overnight), samples were kept in a refrigerator at $4^{o}C$.

All pigs were inspected carefully for any clinical symptoms of a worm burden, expected symptoms being diarrhoea, listlessness and anorexia, and any sign of ill-thrift. Faecal samples from the start of the first balance to the end of the final balance were scored daily for 'softness' on an arbitrary scale 1-10, 1 being the extreme of firmness, and 10 being watery.

2.12 Statistical Analysis

The calorimetry data (Experiment 1) was analyzed firstly by using the split-plot (nested) design as a technique to investigate treatment effects. A further analysis technique, using the 2 x 2 factorial design for each parameter within each time period, investigated any differences between time periods.

In the split-plot design, the effects of two factors, infection and feeding levels, were each tested at two levels in pigs (main plots) at three periods in time (sub-plots). The four treatments, infected high-plane (IH), uninfected high-plane (NH), infected low-plane (IL) and uninfected low-plane (NL) were replicated twice. Pigs (2 per cell) were not re-randomized across periods.

The split-plot experiment assumes that the sub-plot treatments are not randomized over the whole large block, but only over the main plots. Randomization of the sub-plot treatments is assumed to be newly done in each main plot, and the main treatments are assumed to be randomized in the large blocks (Snedecor and Cochran, 1967). The split-plot design gives reduced accuracy on the main-plot treatments, and increased

accuracy on sub-plot treatments and interactions.

In randomized blocks, the model for the split-plot experiment is:

$$X_{ijk} = \mu + M_i + B_j + e_{ij} + T_k + (MT)_{ik} + \ _{ijk}$$

where μ = a general mean

M_i = the fixed effect of the i^{th} infection level; $i = 1, 2, -- a$

B_j = the fixed effect of the j^{th} feeding level; $j = 1, 2, -- b$

$(MB)_{ij}$ = the fixed interaction effect of the i^{th} infection level with the j^{th} feeding level

e_{ij} = random residual error unique to x_{ij}

T_k = the fixed effect of the i^{th} infection level with the k^{th} time period

$_{ijk}$ = random residual error unique to x_{ijk}

For the purpose of hypothesis testing, normality is assumed.

In performing a split-plot analysis, it was recognized that any correlations between errors resulting from repeated measurement on the same pig were ignored. This type of error might affect inferences regarding only the repeated factor (time). Inferences are altered because variation between animals is increased by positive correlation of repeated observations, whereas variation within animals is decreased relative to random variation (Gill and Hafs, 1971).

The 2 x 2 factorial analysis was therefore used in taking inferences from the data regarding differences between time periods.

Regressions were performed on the data in order to produce more information about the physiology of the pig. Tests of homogeneity of the intra-class regressions were performed according to the method of Searle (1971). Where intra-class regressions were adjudged homogeneous, the pooled within-class regression is presented, with its significance tested by the method of Searle (1971).

Experiment 2: Pig Performance, Slaughter and Carcass Characteristics

2.13 Plan of Experiment

The aim of this trial was to provide information on the performance of pigs which had been infected with Oesophagostomum dentatum. Fourteen pairs of pigs were selected and allocated to four treatments, each replicated seven times. The plan of the experiment was a 2 x 2 factorial:

2 sexes (Gilts, Boars)	x	2 levels of infection (Infected, Uninfected)

2.14 Animals and Housing

Seven pairs of Landrace x Large White gilts and seven pairs of Landrace x Large White boars, paired for liveweight from the same litter, were selected from the Massey University Pig Herd. Each member of the pair was randomly allocated to a treatment, either Infected (I) or Uninfected (N), and pigs were moved from the weaner flat-deck house to individual pens when they weighed 16-18kg liveweight. All pigs were treated with anthelmintic and those allocated to the infected treatment were later dosed with 80,000 infective larvae of O. dentatum as in Experiment 1 (Section 2.3).

The trial house was an enclosed building with a concrete floor and surround 28m x 7.5m, and was divided into 28 individual pens, each 1m x 3m. All infected animals were placed on one side of the shed and uninfected animals on the other. Each pig remained in the same pen for the duration of the trial. Boots, shovels and brooms required for use

in the shed were marked and used only for a particular side of the shed.

2.15 Feeding and Management of the Pigs

All pigs were allocated to the 'H' scale of feeding used in Experiment 1 (Appendix 2). The ration was also Massey's Grower ration, and was procured from the same source as for Experiment 1. The pigs were individually fed once daily and water was available ad libitum. There were no refusals, and spillage from the trough to the pen floor was negligible. Pigs were weighed at 0730 hours once weekly, before being fed, and their feed allowance increased on the basis of that liveweight. Those which approached 80 kg liveweight at the weekly weighing were marked and sent to slaughter on the following day.

The preparation of larval cultures, infection of pigs and egg counts in faeces were as for Experiment 1. Collection and examination of dung samples from each pig were done once weekly, in the same manner as for Experiment 1. Pigs were inspected for clinical symptoms of a worm burden as before.

2.16 Recovery of Worms

The section of gut from the stomach to the rectum was removed from each pig shortly after slaughter and transported to the laboratory for examination. There the section from the caecum to the anus was opened and rinsed thoroughly with water. The contents were washed on a sieve of 10 μm aperture size. The washed ingesta was made up to a convenient volume and after thorough mixing a 10% aliquot was removed for worm counting.

The sample thus obtained was examined in the laboratory for the presence of worms.

2.17 Statistical Analysis

The theoretical assumptions underlying the analysis of variance of a factorial experiment for fixed treatment effects are discussed in Snedecor and Cochran (1967).

The data derived from the two levels of infection and two sexes for performance characteristics were subject to the analysis of variance as for a 2 x 2 factorial design.

CHAPTER THREE

RESULTS

3.1 Experiment 1

3.1.1 Pig health and liveweight

All pigs settled into their pens quickly and satisfactorily. They appeared to have little difficulty in adapting to the calorimeter environment. Meal was seldom refused by animals on the high plane of nutrition and never by those animals on the low plane. The low-plane animals seemed more difficult to handle than the high-plane animals, perhaps owing to a degree of stress imposed by underfeeding.

The animals remained in good health, alert and vigorous, for the duration of the trial with one exception. This animal (an uninfected pig) exhibited chronic diarrhoea from about 35 kg liveweight, before its third (final) balance. Therefore data for growth from 3/2/80 to 1/7/80 (20 to 80 kg liveweight) did not include data from this animal.

There was no clinical evidence of parasitism in any animal throughout the experiment. Eggs appeared in the faeces of some animals as early as 19 days after infection and all infections were patent by the 26th day. Egg numbers rose to a maximum concentration ranging between 4,475 and 18,275 eggs per gram (epg) faeces after about 7 weeks, and fell to between 250 and 11,775 epg at slaughter. All uninfected animals remained worm-free.

At the start of experiment 1 liveweight (LW) differences between groups were small (Table 3.1). However, in order to compensate for later differences in LW, the relationships between LW and some metabolic parameters were investigated so as to arrive at a suitable value for the

Table 3.1 Mean liveweight of pigs on each treatment in experiment 1 (± s.e.m.)

Plane of nutrition	High		Low		Level of
Infection treatment	Infected	Uninfected	Infected	Uninfected	significance
Period 1	30.8 (± 1.7)	28.8 (± 0)	27.1 (± 3.7)	26.7 (± 1.3)	ns
2	40.6 (± 2.6)	37.3 (± 0.8)	32.0 (± 3.7	31.6 (± 1.3)	*N
3	49.0 (± 1.7)	46.8 (± 1.5)	41.7 (± 3.9)	41.3 (± 0.5)	ns
Pooled mean liveweight (kg)					
Period 1	28.4 (± 4.2)				
2	35.4 (± 7.4)				
3	44.7 (± 7.0)				

The following notation applies to tables in the text:

N = plane of nutrition.

I = infection treatment.

Period = P = balance interval.

S = sex of animal.

ns = differences between values non-significant.

** = differences between values significant (p 0.01)

* = differences between values significant (p 0.05)

s.e.m. = standard error of the mean.

df = degrees of freedom.

MS = mean square.

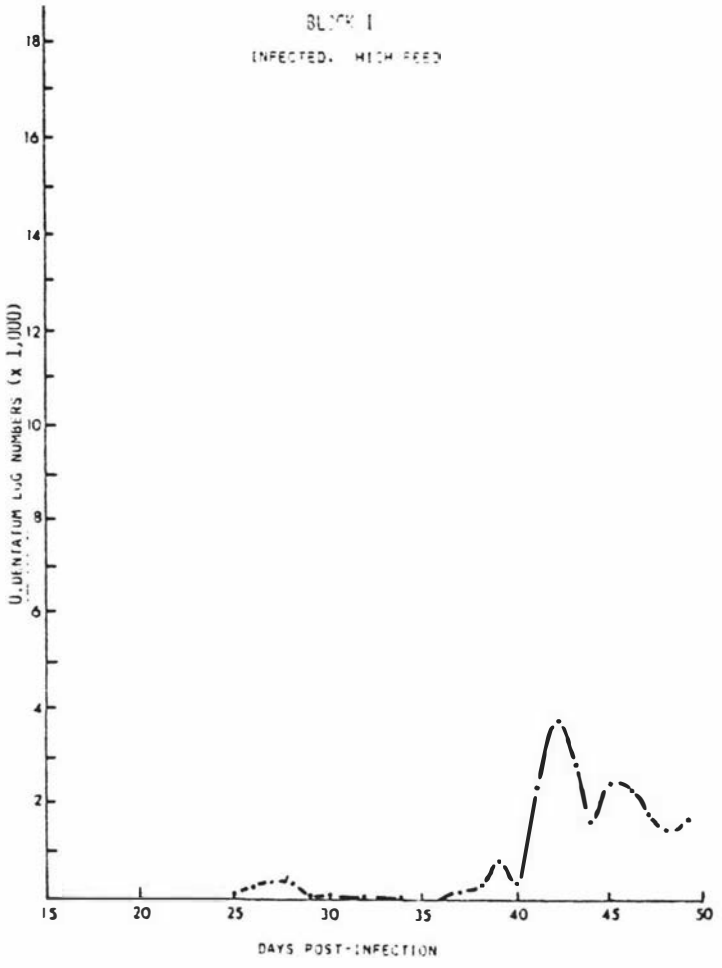
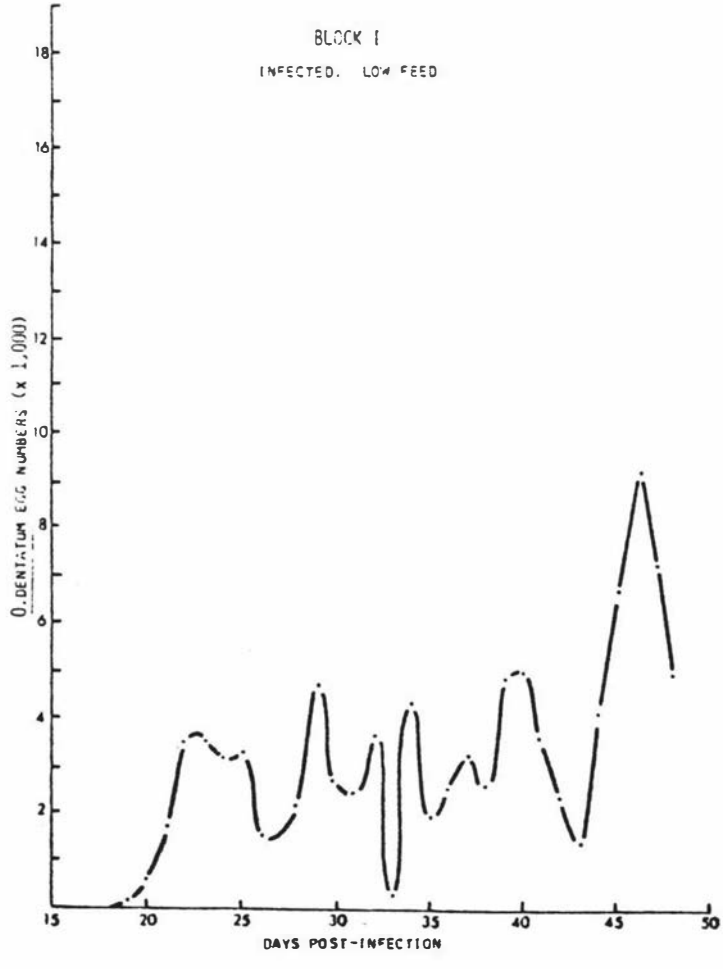


Figure 3.4a (Block I)

O.dentatum egg numbers vs days post-infection for infected pigs in Experiment 1.



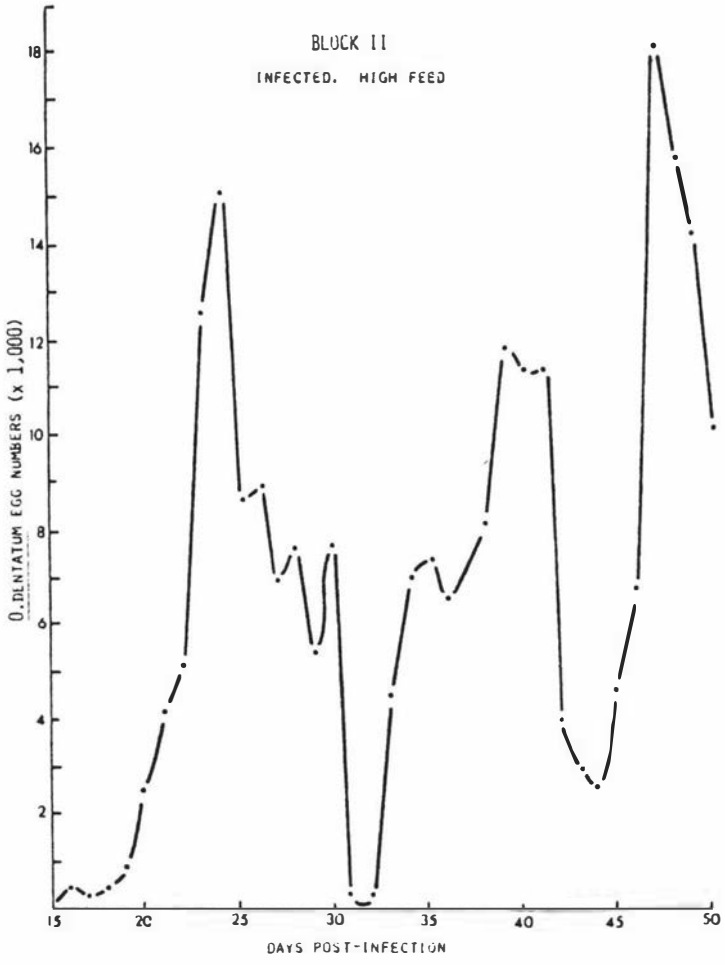
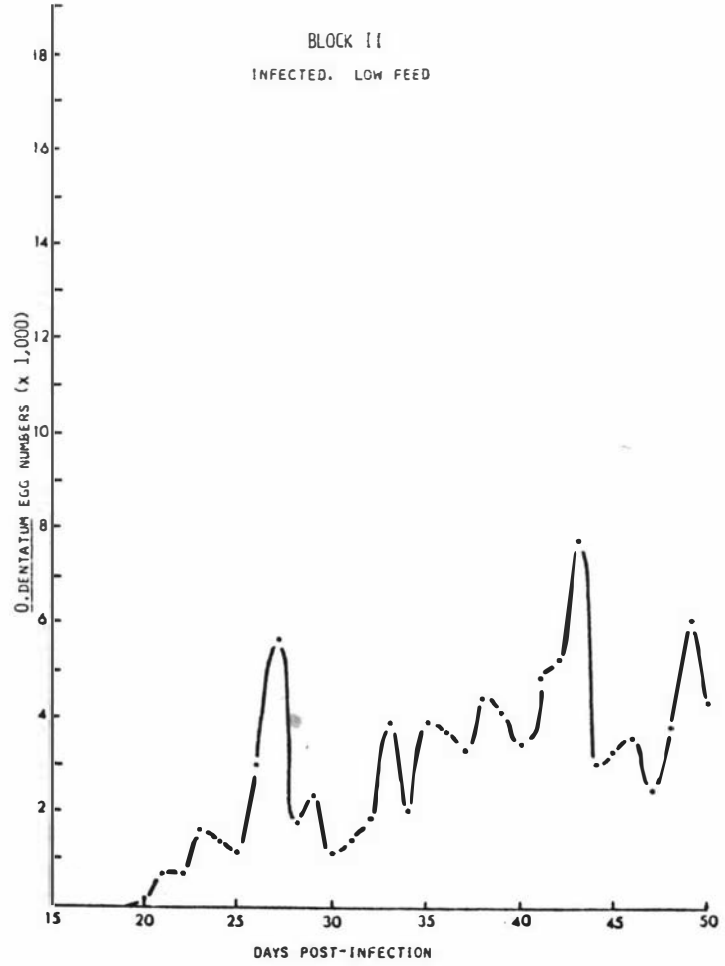


Figure 3.4b (Block II) O.dentatum egg numbers vs days post-infection for infected pigs in Experiment 1.



exponent of LW. For this purpose, all animals' liveweights and feed intakes were first included as experimental data at 6 weeks of age. Data from high-plane animals were included up to 19 weeks of age, and from low-plane animals up to 26 weeks of age. Differences in LW during the trial were attributable to differences in plane of nutrition (Table 3.1) rather than infection with O. dentatum.

For abbreviations found in all Tables, see footnote, Table 3.1.

3.1.2 The relationship between liveweight and various measurements of metabolism

The relationships between liveweight and heat production, nitrogen intake, metabolizable energy intake and energy retention were investigated by regression analysis.

The appropriate exponent for the present data was investigated by regressing each of $\log_{10}$ HP, $\log_{10}$ NI, $\log_{10}$ ME and $\log_{10}$ ER with $\log_{10}$ LW. A suitable exponent is therefore given by the within-class regression coefficient or, where appropriate, the pooled within-class regression coefficient.

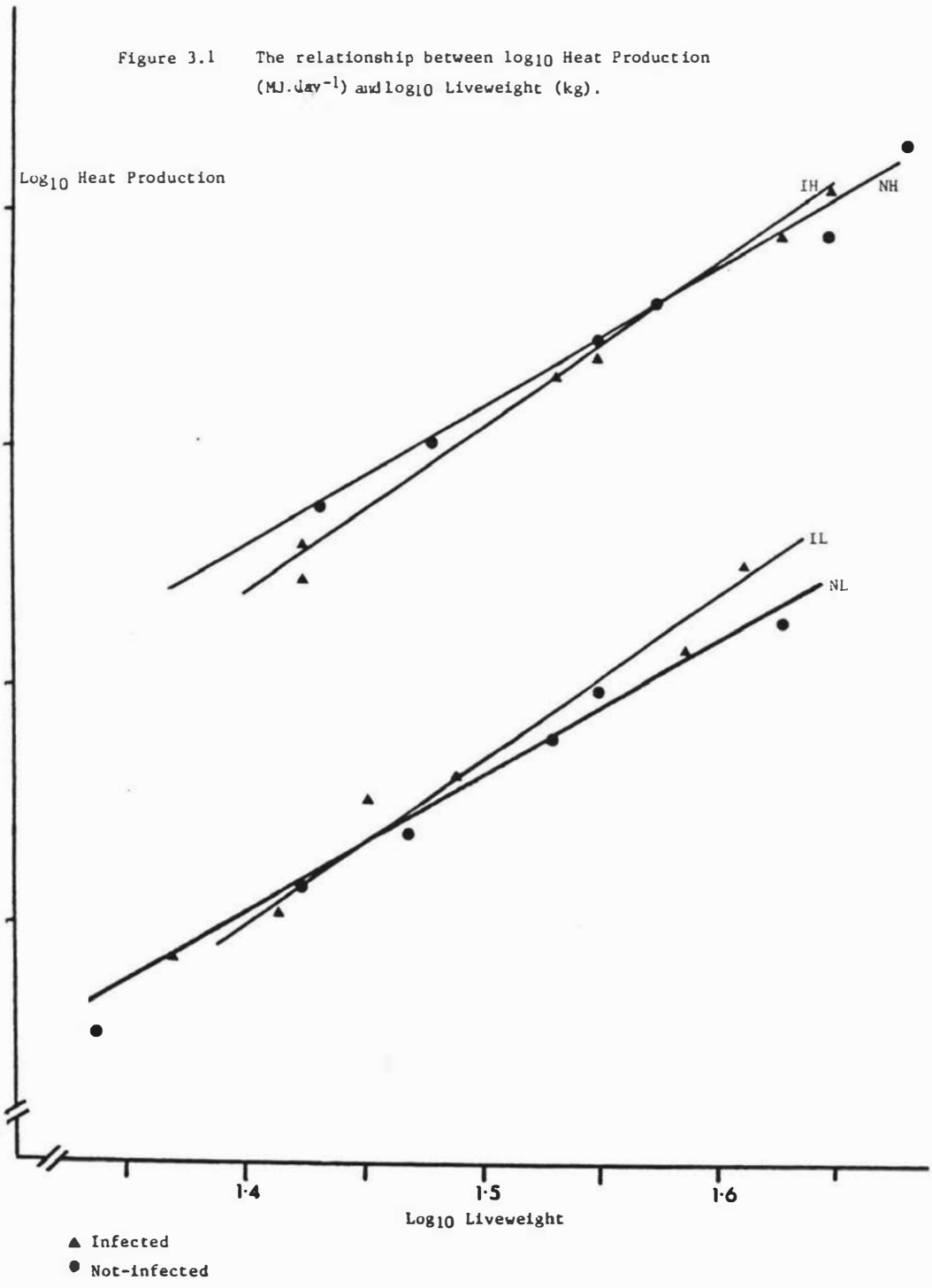
1. Log_{10} HP vs $\log_{10}$ LW

The regression coefficients are presented in Table 3.2a, and tests of homogeneity of within-class regressions are presented in Table 3.2b (Appendix 4). For analytical and comparative purposes a common exponent was necessary for analysis of all the data. Two within-class regression coefficients, that of the uninfected pigs, and high-plane pigs, had confidence limits which did encompass the pooled exponent (Table 3.2a) but which would not encompass the conventionally adopted exponent for LW of 0.75. The remaining two within-class regression coefficients were able to accommodate either possibility. The pooled regression coefficient (0.66) represented the data for all pigs, with

Table 3.2a Regression coefficients calculated by regression analysis of $\log_{10}$ heat production (HP, dependent variable, $MJ.day^{-1}$) on $\log_{10}$ liveweight (LW, independent variable, kg, ± s.e. of coefficient)

Source of data	Regression coefficient	Level of significance	Confidence limits
Infected	0.73 (± 0.03)	**	0.79-0.66
Uninfected	0.60 (± 0.03)	**	0.66-0.53
High-plane	0.65 (± 0.04)	**	0.74-0.56
Low-plane	0.67 (± 0.04)	**	0.76-0.58
Pooled within-class (infection, nutrition)	0.66 (± 0.03)	**	0.72-0.58

Figure 3.1 The relationship between $\log_{10}$ Heat Production ($MJ.day^{-1}$) and $\log_{10}$ Liveweight (kg).



confidence limits which did not encompass 0.75. The widely adopted exponent of 0.75 was closer to the value for infected treatment pigs (0.73) than the value for uninfected pigs (0.60). It was therefore considered that use of the pooled exponent was desirable.

2. Log_{10} NI vs log_{10} LW

The regression coefficients are presented in Table 3.3a, and tests of homogeneity of within-class regressions are presented in Table 3.3b (Appendix 4). The pooled regression coefficient (0.66) is identical to the previously derived value (0.66) for log_{10} HP vs log_{10} LW, supporting this choice as an accurate means of compensating for liveweight differences in comparison of treatment values.

3. Log_{10} ME vs log_{10} LW

The regression coefficients are presented in Table 3.4a, and tests of homogeneity of within-class regressions are presented in Table 3.4b (Appendix 4). The pooled regression coefficient (0.68) was very close to the two previously derived values of 0.66 for log_{10} HP vs log_{10} LW and log_{10} NI vs log_{10} LW.

4. Log_{10} ER vs log_{10} LW

The pooled within-class regression coefficient was not significant, and all within-class regressions were homogeneous (Table 3.5, Appendix 4) i.e. no relationship was found to exist between log_{10} ER and log_{10} LW.

3.1.3 Comparative data for infected and uninfected pigs

Mean values for energy and nitrogen metabolism and growth are presented in Tables 3.6a and 3.7a using the calculated exponent for liveweight of 0.66. Further, Tables 3.6b and 3.7b (Appendix 4) present similar information, calculated using the widely accepted exponent for

Table 3.3a Regression coefficients calculated by regression analysis of $\log_{10}$ nitrogen intake (NI,gms.day^{-1}) on $\log_{10}$ liveweight (LW, kg, ± s.e. of coefficient)

Source of data	Regression coefficient	Level of significance	Confidence limits
Infected	0.70 (± 0.13)	**	0.99-0.40
Uninfected	0.63 (± 0.12)	**	0.89-0.36
High-plane	0.75 (± 0.12)	**	1.02-0.48
Low-plane	0.57 (± 0.12)	**	0.84-0.30
Pooled within-class (infection, nutrition)	0.66 (± 0.08)	**	0.83-0.49

Table 3.4a Regression coefficients calculated by regression analysis of $\log_{10}$ metabolizable energy intake (ME, $MJ.day^{-1}$) on $\log_{10}$ liveweight (LW,kg, $\pm$ s.e. of coefficient)

Source of data	Regression coefficient	Level of significance	Confidence limits
Infected	0.66 ($\pm$ 0.13)	**	0.95-0.37
Uninfected	0.69 ($\pm$ 0.12)	**	0.96-0.42
High-plane	0.61 ($\pm$ 0.12)	**	0.88-0.34
Low-plane	0.75 ($\pm$ 0.12)	**	1.02-0.48
Pooled within-class (infection, nutrition)	0.68 ($\pm$ 0.09)	**	0.87-0.49

Table 3.6a Mean values of energy metabolism for pigs in experiment 1 ($MJ.kg^{-0.66}.day^{-1}$)

Variable	Infected	Uninfected	s.e.m.	Level of significance
Gross energy	2.14	2.15	± 0.02	**N
Faecal energy	0.48	0.49	± 0.02	**N
Urine energy	0.06	0.07	± 0.01	**N
Metabolizable energy	1.60	1.59	± 0.02	**N
DE/GE %	77.5	77.0	± 0.5	ns
ME/GE %	74.7	74.0	± 0.5	ns
ME/DE %	96.5	96.1	± 0.2	ns
Heat production	1.08	1.08	± 0.002	**N *IxN
Energy retained	0.51	0.51	± 0.02	**N
Energy retained as fat	0.43	0.43	± 0.02	**N
Energy retained as protein	0.08	0.08	± 0.005	**N
Respiratory quotient (CO_2 produced/O_2 consumed)	1.12	1.11	± 0.008	ns

Table 3.7a Mean values of nitrogen metabolism and performance for pigs in experiment 1

Variable	Infected	Uninfected	s.e.m.	Level of significance
Nitrogen intake ($gms.kg^{-0.66}.day^{-1}$)	4.21	4.22	± 0.06	**N
Faecal nitrogen ($gms.kg^{-0.66}.day^{-1}$)	0.94	1.01	± 0.06	**N
Urinary nitrogen ($gms.kg^{-0.66}.day^{-1}$)	1.18	1.22	± 0.06	**N
DN/TN %	77.70	76.30	± 1.20	ns
Nitrogen retained ($gms.kg^{-0.66}.day^{-1}$)	2.09	1.98	± 0.12	**N
Liveweight gain ($kg\ day^{-1}$)	0.67	0.64	± 0.03	**N
Mean liveweight (kg)	35.40	36.90	± 1.89	ns
Mean liveweight ($kg^{0.66}$)	10.50	10.80	± 0.37	ns
Feed conversion ratio: 20-80 kg liveweight (kg feed/kg LWG)	3.34	3.59	± 0.14	*N
Average daily gain (kg/day)	0.53	0.56	± 0.06	**N

liveweight of 0.75, to enable the present data to be compared easily with other work. The split-plot design was used in these analyses for reasons outlined earlier (see Materials and Methods, section 2.12).

3.1.4 Utilization of metabolizable energy

Mean values of within-period energy metabolism data are presented for all treatments, using the exponent for liveweight of 0.66, in Table 3.8a. The analyses of variance were performed for a 2 x 2 factorial as outlined in the Materials and Methods, section 2.12.

Similarly, mean values are presented in Table 3.8b (Appendix 4) using the exponent for liveweight of 0.75.

3.1.5 Energy retention

Measurements of energy retained for all treatments in each of three balance periods are compared in Table 3.9a, using the calculated exponent for liveweight of 0.66. Similar comparisons are presented in Table 3.9b (Appendix 4) using the exponent 0.75.

3.1.6 Nitrogen metabolism

Mean values of nitrogen metabolism for all treatments in each of three balance periods are presented in Table 3.10a using the calculated exponent for liveweight of 0.66. Included for comparative purposes is Table 3.10b (Appendix 4) which presents estimates using the exponent for liveweight of 0.75.

3.1.7 Faecal consistency

A method of point-scoring was applied to a faeces sample collected daily from each pig, for the first five weeks in which infections were patent. The scoring was subjective, taken on a scale ranging from 1 (very hard) to 10 (watery). The results are shown in Table 3.11, pooled across feeding levels.

Table 3.8a Mean values of several measurements of energy metabolism ($MJ.kg^{-0.66}.day^{-1}$)

Plane of Nutrition	High		Low			Level of
Infection treatment	Infected	Uninfected	Infected	Uninfected	s.e.m.	significance
DE/GE %	76.93	6.85	77.98	77.19	± 0.69	ns
ME/DE %	96.27	95.99	96.68	96.13	± 0.36	ns
Metabolizable energy intake						
Period 1	1.89	1.97	1.29	1.29	± 0.05	**N
2	1.99	1.98	1.21	1.18	± 0.08	**N
3	1.92	1.87	1.26	1.23	± 0.10	**N
Heat production						
Period 1	1.23	1.28	0.87	0.90	± 0.01	*I*N
2	1.26	1.25	0.93	0.91	± 0.02	**N
3	1.26	1.25	0.94	0.89	± 0.03	**N

Table 3.9a Mean values of several measurements of energy retained ($MJ.kg^{-0.66}.day^{-1}$)

Plane of nutrition	High		Low			Level of
Infection treatment	Infected	Uninfected	Infected	Uninfected	s.e.m.	significance
Energy retained						
Period 1	0.66	0.69	0.40	0.39	± 0.03	**N
2	0.73	0.73	0.28	0.27	± 0.07	**N
3	0.66	0.62	0.32	0.34	± 0.11	*N
Energy retained as fat						
Period 1	0.56	0.60	0.34	0.33	± 0.02	**N
2	0.64	0.65	0.20	0.21	± 0.08	**N
3	0.55	0.53	0.27	0.29	± 0.09	*N
Energy retained as protein						
Period 1	0.09	0.09	0.06	0.06	± 0.02	*N
2	0.09	0.08	0.07	0.06	± 0.02	ns
3	0.11	0.10	0.06	0.02	± 0.02	*N
ER (MJ/kg LWG)	9.54	10.07	6.43	6.93	± 1.30	*N

Table 3.10a Mean values of several measurements of nitrogen metabolism (gms.kg$^{-0.66}$.day^{-1})

Plane of nutrition	High		Low			Level of
Infection treatment	Infected	Uninfected	Infected	Uninfected	s.e.m.	significance
Nitrogen intake						
Period 1	4.99	5.18	3.20	3.25	± 0.4	**N
2	4.91	4.83	3.53	3.47	± 0.3	**N
3	5.39	5.40	3.21	3.19	± 0.4	**N
Urinary N excreted						
Period 1	1.28	1.32	1.04	1.01	± 0.06	**N
2	1.29	1.25	0.87	1.03	± 0.1	*N
3	1.56	1.61	1.02	1.11	± 0.2	*N
N retained						
Period 1	2.46	2.47	1.52	1.55	± 0.4	ns
2	2.35	2.19	1.89	1.66	± 0.4	ns
3	2.80	2.57	1.51	1.41	± 0.5	*N
Digestibility of N						
$DN/_{TN}$ x 100 (%)	76.6	73.9	78.8	78.6	-	ns

Table 3.11 Consistency of faeces from infected and uninfected pigs (mean scores)

Weeks of patency	Infected score	Uninfected score
Block I		
1	5.3	5.0
2	5.5	5.8
3	4.7	5.1
4	4.4	4.8
5	4.7	5.0
Block II		
1	5.0	4.9
2	5.1	5.0
3	5.1	5.0
4	4.9	5.0
5	4.5	7.6†

† scouring animal's values included here.

3.1.8 The investigation of energy and nitrogen metabolism by regression

Heat production, energy retained, energy retained as fat, energy retained as protein and nitrogen retained were regressed with metabolizable energy intake and nitrogen intake. Where applicable, corresponding tests of homogeneity of the within-class (infection treatment, plane of nutrition) regressions were also presented. The overall regression and regressions for each infection treatment pooled over feeding levels were used to provide particular information regarding the use of energy for all pigs, and for each infection treatment.

The results of the overall regression of HP vs ME, and the regression of HP vs ME for each infection treatment pooled over feeding levels are shown in Table 3.12 and Fig. 3.2. Similarly regressions are presented for ER vs ME (Table 3.13, Fig. 3.3) and ERF vs ME (Table 3.14). The regression of ERP vs ME resulted in only a single significant regression equation (Table 3.15).

The further investigation of the metabolism of nitrogen involved regression analysis as introduced earlier (the metabolism of energy and nitrogen, p. 98).

ERP vs NI

The regression coefficients are presented in Table 3.16a, and tests of homogeneity of within-class regressions are presented in Table 3.16b (Appendix 4).

Multiple regression equations relating ER to ME and NI using the exponent for liveweight of $kg^{0.66}$ are presented in Table 3.17a, and the corresponding equations using $kg^{0.75}$ are presented in Table 3.17b (Appendix 4). Similarly, multiple regression equations relating ME

Table 3.12 Results of regression analysis of heat production (HP, $MJ.kg^{-0.66}.day^{-1}$) on metabolizable energy intake (ME, $MJ.kg^{0.66}.day^{-1}$).

Source of data	Regression equation	Level of significance
Infected	HP = 0.44ME + 0.40 ($\pm$ 0.12)	**
Uninfected	HP = 0.48ME + 0.34 ($\pm$ 0.12)	**
Overall	HP = 0.46ME + 0.37 ($\pm$ 0.08)	**

Table 3.13 Results of regression analysis of energy retained (ER, $MJ.kg^{-0.66}.day^{-1}$) on metabolizable energy intake (ME, $MJ.kg^{-0.66}.day^{-1}$)

Source of data	Regression equation	Level of significance	ME at ER = 0
Infected	ER = 0.56ME - 0.40 ($\pm$ 0.12)	**	0.71
Uninfected	ER = 0.53ME - 0.35 ($\pm$ 0.12)	**	0.66
Overall	ER = 0.54ME - 0.37 ($\pm$ 0.08)	**	0.69

Figure 3.2 Graph of Heat Production vs Metabolizable Energy Intake for Infected and Uninfected pigs.

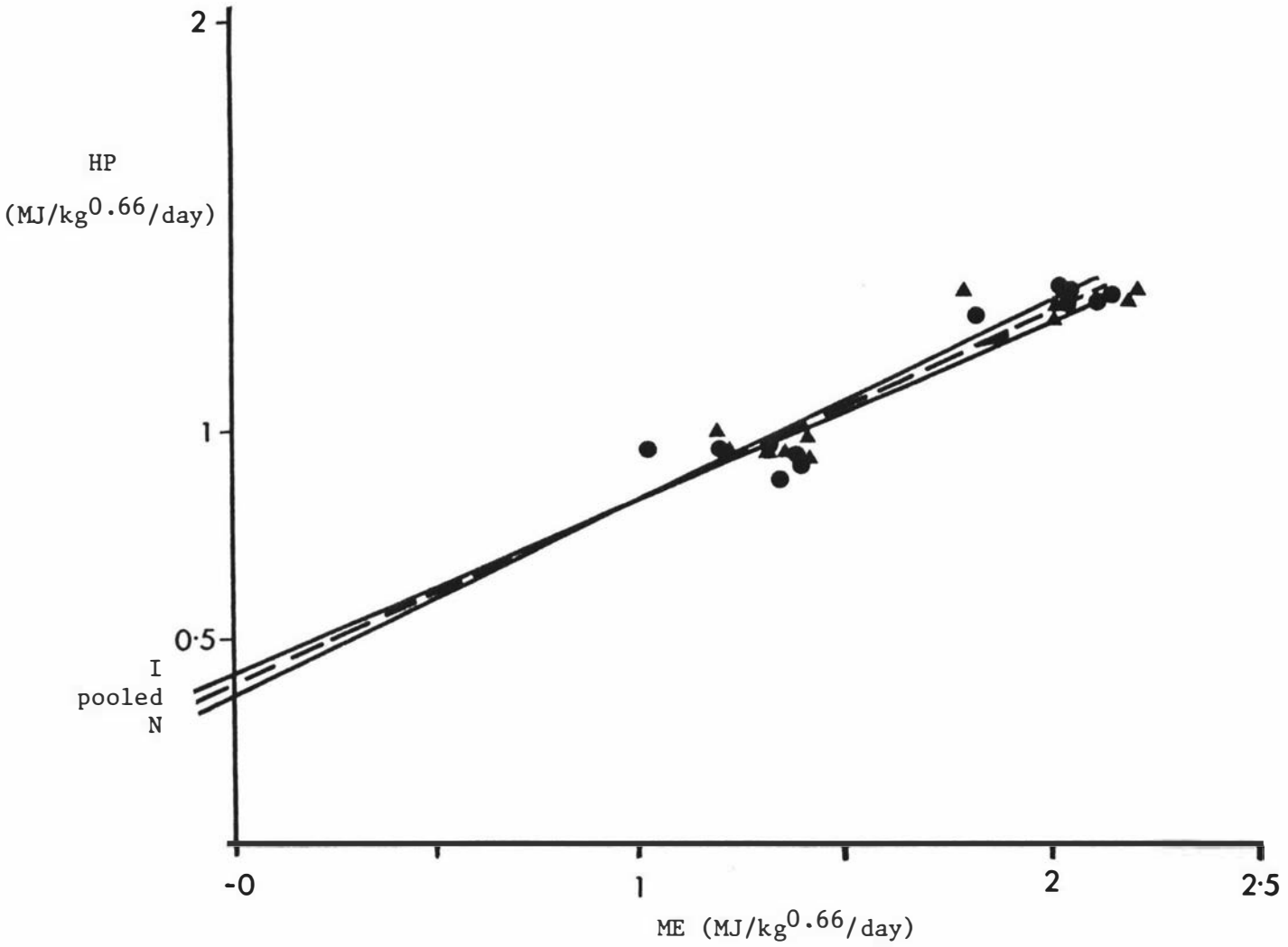
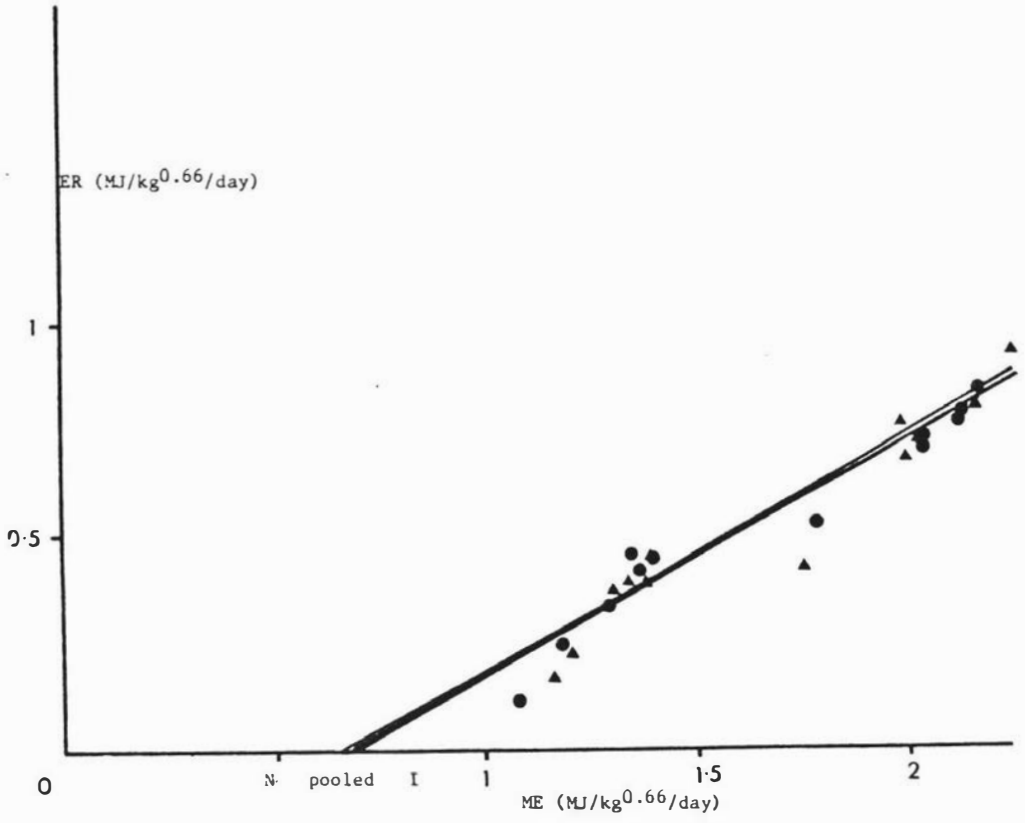


Figure 3.3 Graph of Energy Retained vs Metabolizable Energy Intake for Infected and Uninfected pigs.



▲ Infected

● Uninfected

Table 3.14 Results of regression analysis of energy retained as fat (ERF, $MJ.kg^{-0.66}.day^{-1}$) on metabolizable energy intake (ME, $MJ.kg^{-0.66}.day^{-1}$)

Source of data	Regression equation	Level of significance
Infected	ERF = 0.36ME - 0.11 ($\pm$ 0.12)	*
Uninfected	ERF = 0.49ME - 0.35 ($\pm$ 0.12)	**
Overall	ERF = 0.43ME - 0.24 ($\pm$ 0.08)	**

Table 3.15 Results of regression analysis of energy retained as protein (ERP, $MJ.kg^{-0.66}.day^{-1}$) on metabolizable energy intake (ME, $MJ.kg^{-0.66}.day^{-1}$)

Source of data	Regression equation	Level of significance
Uninfected	ERP = 0.04ME + 0.01 ($\pm$ 0.12)	**

Table 3.16a Regression coefficients calculated by regression analysis of energy retained as protein (ERP, $MJ.kg^{-0.66}.day^{-1}$) on nitrogen intake (NI, $gms.kg^{-0.66}.day^{-1}$)

Source of data	Regression coefficient	Level of significance
Infected	0.04 ($\pm$ 0.005)	**
Uninfected	0.034 ($\pm$ 0.006)	**
High-plane	0.036 ($\pm$ 0.004)	**
Low-plane	0.049 ($\pm$ 0.009)	**
Pooled within-class (infection, nutrition)	0.038 ($\pm$ 0.004)	**

Table 3.17a Multiple regression equations relating energy retained (ER, $MJ.kg^{-0.66}.day^{-1}$) to metabolizable energy intake (ME, $MJ.kg^{-0.66}.day^{-1}$) and nitrogen intake (NI, $MJ.kg^{-0.66}.day^{-1}$)

Source of data	Regression equations
Infected	$ER = 0.77ME^{**} - 0.09NI^{*} - 0.36$ ($\pm$ 0.10) ($\pm$ 0.04)
Uninfected	$ER = 0.74ME^{**} - 0.09NI^{*} - 0.29$ ($\pm$ 0.08) ($\pm$ 0.03)
Pooled within-class (infection, nutrition)	$ER = 0.76ME^{**} - 0.09NI^{**} - 0.32$ ($\pm$ 0.06) ($\pm$ 0.02)

ME, NI : r = 0.88

to ERF and ERP using the exponent $kg^{0.66}$ are presented in Table 3.18a, and the corresponding equations using $kg^{0.75}$ are presented in Table 3.18b (Appendix 4). It should be noted that the supposedly independent variables in the equations were correlated.

Mean values of liveweight gain for pigs of each treatment are shown for individual balance periods in Table 3.19. Values for feed conversion ratio are for the period 20 to 80 kg liveweight.

3.2 Experiment 2

3.2.1 Pig health

Infected animals showed no clinical signs of infection; nevertheless, eggs appeared in the faeces at approximately 3 weeks post-infection, rose to a maximum concentration ranging between 2,825 and 36,250 (average 19,907) epg faeces at 6-13 weeks, and fell to between 50 and 25,825 (average 11,060) epg faeces at slaughter. Adult worm populations at slaughter ranged from 70 to 9,200 (average 4,255) worms/pig (Appendix 5). Numerous small, firm nodules approximately 1mm diameter were seen in the wall of the colon of all infected pigs. All 28 animals remained in good health, alert, vigorous and active for the duration of the growth trial. No O. dentatum eggs or worms were recovered from uninfected pigs.

3.2.2 Comparative data for infected and uninfected pigs

Mean values for several measurements of performance and carcass quality are shown in Table 3.20. The results of analyses of variance are given for differences between infection treatments and for differences between two sexes (boars and gilts). Table 3.20 showed that no differences developed between infected and uninfected pigs for any of the parameters measured. However, significant differences were

Table 3.18a Multiple regression equations relating metabolizable energy intake (ME, $MJ.kg^{-0.66}.day^{-1}$) to energy retained as fat (ERF, $MJ.kg^{-0.66}.day^{-1}$) and as protein (ERP, $MJ.kg^{-0.66}.day^{-1}$)

Source of data	Regression equations
Infected	$ME = 1.41ERF^{**} + 4.63ERP^{*} + 0.63$ ($\pm$ 0.17) ($\pm$ 1.47)
Uninfected	$ME = 1.52ERF^{**} + 5.48ERP^{**} + 0.52$ ($\pm$ 0.12) ($\pm$ 1.07)
Pooled within-class (infection, nutrition)	$ME = 1.46ERF^{**} + 4.99ERP^{**} + 0.58$ ($\pm$ 0.10) ($\pm$ 0.85)

ERF, ERP : r = 0.48

Table 3.19 Mean values of liveweight gain for pigs on each treatment in experiment 1

Plane of nutrition	High		Low		Level of
Infection treatment	Infected	Uninfected	Infected	Uninfected	significance
Liveweight gain (grams/day)					
Period 1	0.66 (±0.06)	0.66 (±0.01)	0.46 (±0.08)	0.54 (±0.01)	ns
2	0.80 (±0.01)	0.76 (±0.03)	0.52 (±0.06)	0.53 (±0.01)	**N
3	0.85 (±0.01)	0.97 (±0.10)	0.56 (±0.06)	0.54 (±0.1)	*N
Feed conversion ratio: 20-80 kg (kg feed/ kg LWG)	3.13 (±0.1)	3.36 (±0.02)	3.49 (± 0)	4.19 †	ns

† only one value included.

Table 3.20 Mean values for performance, carcass quality and worm numbers for pigs in experiment 2.

Variable	Infected	Uninfected	s.e.m.	Level of significance
Initial liveweight (kg)	21.00	21.00	± 0.30	ns
Final liveweight (kg)	82.30	82.10	± 0.40	ns
ADG : 20-50 kg LW (kg/d)	0.66	0.64	± 0.01	ns
ADG : 50-80 kg LW (kg/d)	0.81	0.79	± 0.02	*S
ADG : 20-80 kg LW (kg/d)	0.73	0.70	± 0.01	*S
FCR : 20-80 kg LW (kg feed/kg LWG)	2.90	3.00	± 0.05	*S
Carcass weight (hot, kg)	61.50	61.10	± 0.30	ns
Carcass weight (cold, kg)	60.20	59.90	± 0.40	ns
Killing out percentage (hot)	73.10	73.00	± 0.30	ns
Killing out percentage (cold)	74.70	74.40	± 0.30	ns
Maximum shoulder fat (mm)	33.00	34.60	± 0.60	ns
Minimum loin fat (mm)	16.50	16.60	± 0.60	*S
Fat over the eye muscle - C(mm)	14.80	15.60	± 0.60	ns
Fat over the eye muscle - K(mm)	23.50	26.40	± 0.90	ns
Width eye muscle (mm)	88.80	86.60	± 0.90	ns
Depth eye muscle (mm)	46.70	50.10	± 1.10	ns
Area eye muscle (cm^2)	30.50	31.30	± 0.60	ns
Back rasher ratio	0.77	0.81	± 0.03	ns
Egg numbers (average)	11,060	0		
Worm numbers at slaughter	4,255	0		

recorded for some parameters, and were attributable to the difference in performance of the two sexes.

CHAPTER FOUR

DISCUSSION

4.1 The Pattern of Infection with O.dentatum

Infections first became patent 19-26 days after larval dosage. A similar minimum prepatent period (21 days) was recorded by Pattison et al. (1980) although there was some variation between animals. Other workers have recorded prepatent periods varying from 26-28 days (Poelvoorde, 1978a) to 6-7 weeks (Hass et al, 1972). There are several possible explanations for these differences in results, such as variation in the sensitivity of techniques used to detect eggs, possible variations in host resistance or strains of parasite.

In both the present experiments, egg counts fluctuated widely in individual animals (see sections 3.1.1, 3.2.1) and varied considerably between animals. Pigs in experiment 1 on the low plane of nutrition did not have consistently higher egg counts than animals on the high plane of nutrition (Figs. 3.4a, 3.4b). Similar variations in worm egg output have been observed by other workers (Pattison et al, 1980; Poelvoorde, 1978a).

In experiment 2 of the present study, examination of the digestive tracts from all animals revealed that only infected animals carried O.dentatum (see Chapter 3, section 3.2.1). Very high numbers were recovered from some individuals but there was a wide variation in worm numbers, despite the use of one uniform infective dose. It should be noted that the worm burdens present at slaughter were likely to have been lower by some unknown amount than they had been earlier, since some worms would already have been lost.

It was clear from the data that, in general, pigs which excreted

large numbers of parasitic eggs in their faeces also yielded high numbers of adult parasites at slaughter, and those with low parasitic egg production had low numbers of adult parasites at slaughter ($r = 0.59$; see Appendix 5). However, this could only be regarded as a very general guide, and egg production data would not appear to be suitable for very precise prediction of worm populations. A similar pattern of infection could be expected to have existed in pigs in experiment 1. High egg counts indicate that in all animals a substantial, if variable, worm burden was established (Figs. 3.4a; b).

A further experiment, using the same isolate of O.dentatum, and a similar dose of 80,000 larvae, was subsequently conducted by Smith and Charleston (unpublished; see Table 4.1) with four groups each of eight pigs. Each group comprised four gilts and four boars. In infected pigs, the mean worm burden at slaughter (4,269) was similar to the 4,255 recorded in experiment 2. Once again no significant differences could be found between infected and uninfected pigs for various performance parameters investigated (Table 4.1). This evidence supports the results of the earlier experiments 1 and 2.

Pattison et al (1980) found in growing pigs mean worm burdens at slaughter of 5,610, 5,432 and 5,588 for three different infection levels, giving significantly reduced growth rate, efficiency of feed conversion and lowered backfat depths.

There are problems of a disgnostic nature reflected in these conflicting results.

In the present experiments, and in those of Pattison et al (1980), subclinical levels of O.dentatum were established by use of similar doses of the same parasite. Much higher egg counts were recorded for the present data (maximum average of 11,060) eggs per gram faeces) compared

Table 4.1 Mean performance of group fed infected and uninfected pigs (From: Smith and Charleston, unpublished)

Variable	Infected	Uninfected	s.e.m	Level of significance
Daily gain (kg)	0.676	0.675	± 0.007	ns
Feed conversion ratio	2.73	2.74	± 0.034	ns
Killing-out percentage	76.24	75.39	± 0.400	ns
Intrascope fat measurement (mm)	13.25	15.07	± 0.376	ns
Worm burden at slaughter	4,269	nil	-	-

with a maximum average of 2,400 eggs per gram faeces given by Pattison et al (1980). Both experiments had similar worm burdens at slaughter. Nevertheless, in the present experiments, the performance of the pigs showed no adverse effects, whereas in the experiments of Pattison et al (1980) performance was adversely affected by infection. It is apparent then, that such high faecal egg counts do not necessarily indicate that the performance of the host is being adversely affected. It is interesting to note also that Pattison et al (1980) found that increasing the larval dose, although causing increased effects on pig performance, did not result in higher worm burdens at slaughter, approximately 9 weeks later. This suggests some regulation of the adult worm burden established following single dose infection, and that the increasing effect of higher infection rates on production parameters must have been due to the greater larval challenge in the early stage rather than to the adults (Pattison et al, 1980).

In the growing pig, clinical disease has been reported in pigs infected artificially by dosing with 25,000 to 80,000 larvae (Nickel and Haupt, 1964; Davidson and Taffs, 1965). On the other hand, there are reports that pigs have tolerated, with no adverse effect on health, larval levels of up to 20,000 (Nickel and Haupt, 1964), 30,000 (Jacobs, 1969) and 100,000 (McCracken and Ross, 1970).

No clinical signs of oesophagostomiasis such as anorexia (Table 3.8a), anaemia, listlessness or change in faecal consistency (Table 3.11) were observed in the present studies. The general health of animals on both trials appeared to be good, with the exception of one case of diarrhoea in an uninfected animal.

One can only speculate on the possible causes for such conflicting reports. The likelihood of a relationship between site of infection and effect on pig performance must be ruled out in infections with

O.dentatum, since the parasite always inhabits the anterior portion of the colon (Jacobs, 1967a).

Possible reasons for differing reports may be differences between the strains of parasite used and differences between the genotypes of pig used in the studies. Another possibility is that the parasite produces some 'factor' which is actually useful to the pig.

4.2 The Relationship Between Liveweight and Various Measurements of Metabolism in Experiment 1

The metabolism of energy and nitrogen is considered to vary with an exponent of liveweight (Klieber, 1965; McDonald et al, 1973). Conventionally the exponent of 0.75 for liveweight is chosen (Klieber, 1965), although strictly this only applies to mature, fasted animals.

Although selection was made so that animals in experiment 1 should be very similar in bodyweight, some differences were inevitable, both initially and subsequently during the experiment. In order to detect any treatment effects with greater precision, it was necessary to reduce variation in the data caused by variation in liveweight within and between treatments.

The relationships between liveweight and various measurements of metabolism were investigated (Chapter 3, section 3.1.2). Both ME and HP were found to be proportional to $LW^{0.66}$, so that 0.66 was considered to be the most satisfactory exponent of LW to reduce the variation caused by liveweight differences within and between balance periods for these data. Work by other authors has shown a range of exponents which have been measured and used in various studies (Table 4.2).

Many other authors use 0.75 as an adopted convention, even though their data may show another value to be more 'accurate', e.g. Jordan

Table 4.2 Exponential functions which reduce variation in data caused by liveweight differences

Exponent used (kg^{exp})	Pig liveweight (kg)	Source
0.57	16 - 196	Brierem (1936)
0.8	34 - 64	Holmes and Mount (1967)
1.0	17 - 34	Holmes and Mount (1967)
0.57	20 - 90	Fuller and Boyne (1970)
0.75; 0.67; 0.57	25 - 110	Thorbek (1973)

and Brown (1970), Thorbek and Henkel (1976), Carr, Boorman and Cole (1977), Holmes and Close (1977), Close et al, (1978), McCracken et al (1980) and Holmes et al (1979).

4.3 The Consequences of Infection with O.dentatum

In order to investigate the partitioning of food energy and nitrogen by infected and uninfected animals, regression analyses were performed on data from experiment 1. Heat production, energy retained and nitrogen retained represent the partitioning of food energy and nitrogen into use for maintenance or use for productive purposes. A further consequence of this use of energy and nitrogen is that where retention occurs, it takes place as either fat or protein.

Two different techniques in regression analysis were used. The first represents a line drawn through the data unadjusted for treatment effects (e.g., Table 3.12, Fig. 3.2). This technique was useful in increasing accuracy of inferences taken by extrapolation of the line formed, due to wide separation of feeding levels. The second technique represents the relationship between two parameters after adjustment for treatment effects.

Very little literature has been published on the metabolic effects of O.dentatum infections. Dargie (1979), in a general review of many diverse parasites, emphasised that differences between experimental conditions make critical comparisons between experiments impossible, and that for different infections the appropriate data are not available. In reviewing diverse data, he concluded that several features were indicated. Firstly, each parasite he examined was capable of impairing growth and/or causing loss of weight; therefore these effects were independant of the site of infection. Secondly, the heavier the

infection the more dramatic is the effect. Finally, young or poorly fed animals are more severely affected than their older counterparts or those maintained on a better diet, but carrying the same worm burden.

1. Gross energy intake

In the present studies, the maximum feeding level was 90% of appetite rather than ad libitum. Anorexia was not observed; however, it might have been detectable in pigs fed ad libitum. Analyses of the three balance periods in experiment 1 were performed both collectively (split-plot) and for separate balance periods (factorial), though not all analyses are shown in the results section. Tables 3.6a, 3.7a and 3.8a (Chapter 3) show that for the infected animals, a worm burden did not induce anorexia either by larval development or the presence of adult worms.

Results of published pair-feeding experiments invariably show that reduced feed intake caused by infection *per se* is an important contributor to impaired production with a wide range of parasites, accounting for anything between 40% and 90% of the observed weight differences between infected and ad libitum fed controls (Dargie, 1979). The precise cause of anorexia is unknown (Charleston, 1976; Dargie, 1979).

Anorexia has been recorded in infections with *O.dentatum* (Kaarma, 1974; Shorb, 1948). Many other reports confirm anorexia (Fitzsimmons, 1969; Barger, 1973; Roseby, 1973; Reveron *et al.*, 1974; Sinclair, 1975; Berry and Dargie, 1976; Sykes *et al.*, 1980) in other hosts infected with a diversity of other parasites.

2. The digestibility of dietary energy and nitrogen

There was no measurable effect of infection on digestibility due to infection in either experiment (Tables 3.6a, 3.7a, 3.8a and 3.20, Chapter 3).

Other experimental work with O.dentatum has produced conflicting results. For instance, Kaarma (1974) found an infective dose of 100,000 larvae resulted in a decrease in digestibility of organic matter of 3% and 5.2% in two experiments respectively. He also recorded a decrease in apparent digestibility of nitrogen. Pattison et al (1980) also noted changes in digestibility with a similar dose of 100,000 O.dentatum larvae. Their experiment resulted in a decrease in apparent digestibility of dry matter, organic matter, gross energy and crude fibre. However, other experiments using artifical infections of O.dentatum (Shorb, 1948; Nickel and Haupt, 1964; Schnaidmiller, 1969; Hass et al, 1972; Poelvoorde and Berghen, 1978; 1979a; 1979b) did not measure any of the changes recorded by Kaarma (1974) or Pattison et al (1980). It is clear, however, that the present results do not concur with those experiments recording decreased digestibilities in infected pigs. The present experiments and that of Pattison et al. (1980) were similar in many respects, so the discrepancy between results is especially noteworthy.

A number of mechanisms have been suggested whereby subclinical parasitism might affect the nutrition of the host, particularly reduced absorption, an increased rate of flow of digesta and reduced enzyme activity. However, Symons (1969) has pointed out that although lesions of oesophagostomiasis have been described, it is not easy to accept that this infection has a serious effect on digestion and absorption, since the duodenum and jejunum are not involved. A decrease in the absorption of materials has been shown to occur in a number of host/parasite systems, for example in nematode infection in calves (Hammond and Worley, 1969) but this always appears to be linked to tissue disruption in the absorption site, mainly the small intestine. However,

while other experiments have even shown changes in enzymic activity in cells of the parasitized intestinal mucosa of rats and sheep (Symons, 1966; Symons and Jones, 1970; Coop and Angus, 1975) attempts to demonstrate impaired digestion and absorption of protein, maltose, glucose and histidine have failed. Contrary to once widely held views, evidence indicates that digestive efficiency per se is comparatively little affected by gastrointestinal nematode parasitisms (Charleston, 1976a). These conclusions concur with the results of the present studies but not with those of Pattison et al (1980).

3. Heat production

Experiment 1

There was no significant difference between infected and uninfected pigs for HP over all balance periods (Table 3.6a). However, HP was significantly lower in infected pigs in the first balance period (Table 3.8a), although there were no differnces between infected and uninfected pigs in the two subsequent balance periods. These results indicated a relative change in HP between infection groups, but which gave no overall significant difference.

An I x F interaction was present in addition ($F_{1,3} = 22.7$, $p < 0.05$, Table 3.6a), which meant that infected animals had a higher HP than uninfected animals at the low feeding level, whereas they had a lower HP than uninfected animals at the high level of feeding.

Overall HP results ($MJ.kg^{-0.66}.day^{-1}$)

Infection treatment	Plane of Nutrition		
	High	Low	
Uninfected	1.2577	0.8983	0.3394
Infected	1.2508	0.9114	0.3594
	0.0069	-0.0131	

Regression analysis indicated that HP increased with liveweight at significantly different rates for infected pigs (0.73 $MJ.kg.^{-1}day^{-1}$, $t_{0.1,10}$) in comparison with uninfected pigs (0.60 $MJ.kg.^{-1}day^{-1}$, $t_{0.1,10}$, Table 3.2a, Fig. 3.1). This difference in rate of increase resulted in HP at the end trial being higher in infected pigs (although not statistically significantly higher) then in uninfected pigs. Therefore, there was a relative change in HP values for infected and uninfected pigs during the trial.

The overall conclusion from these results must be that infection did not alter HP significantly over the whole trial. However, the significantly lower HP for infected pigs in balance 1 is an interesting result. It is possible that the infection caused the pigs to reduce their physical activity, which resulted in a decrease in HP. A similar analysis using 0.75 as an exponent failed to produce any significant difference in $HP/kg^{0.75}$ between infection levels. This analysis would be expected to be less sensitive than that using the exponent $W^{0.66}$, derived directly from the data. The I x F interaction indicates that low-plane infected pigs may have been adversely affected by infection in comparison with low-plane uninfected pigs. However, it is rather more difficult to explain the lowered HP in high feed infected pigs in comparison with the high feed uninfected pigs.

The results which show that HP altered with LW at significantly different rates for different infection treatments might be interpreted to mean that the demand for energy and/or protein was significantly different for different infection treatments. This supports the statements of Dargie (1979) presented earlier (section 4.3). Regression analysis, however, indicated that HP altered with ME similarly for infected and uninfected pigs (Table 3.12, Fig. 3.2), and that ERP

altered with NI similarly for both infection treatment pigs (Table 16a). These results do not support the results showing significant differences in rate of change of HP with LW.

One must accept, therefore, that the utilization of energy and nitrogen were not significantly changed by infection with O.dentatum.

4. Faecal consistency

In experiment 1 of this study, a method of point scoring of faecal consistency (Table 3.11) was adopted. This was considered useful in recording obvious differences in faecal consistency which might have occurred during the experiment. Some variation in faecal consistency was observed (Figs. 3a, b; Table 3.11). Variation in faecal consistency was very similar within infected and uninfected treatments (excluding week 5, block II, Table 3.11), and between infection treatments for each week (excluding week 5, block II, Table 3.11). The excluded figures relate to one uninfected animal which developed a chronic scour. The scour undoubtedly biased the faecal score figures.

Observation of faeces from pigs in experiment 2 likewise failed to detect evidence of scouring caused by infection. Charleston (1976a) observed that little is known of the cause of diarrhoea in nematode infections of the small and large intestines. A limitation of the analysis method used in the present experiments was that any energy and nitrogen determinations on the faeces would have included any parasitic component present in the faeces. It was thus impossible to determine any contribution of the parasite to the energy or protein content of the faeces.

5. The metabolism of nitrogen

The metabolism of nitrogen in experiment 1 is summarized

in Table 3.10a. Infection with O.dentatum did not significantly alter the intake, digestibility (see this section, part 2), urinary excretion or retention of nitrogen in comparison with uninfected animals. The regression coefficients of ERP vs NI (Table 3.16a) are shown for data adjusted for treatment effects. The pooled within-class regression was significant ($t_{22} = 9.5$, $p < 0.01$) and all within-class regressions were homogeneous. This result shows that there was no difference in the utilization of nitrogen for protein deposition between infection treatments.

Pigs in experiment 2 did not show any differences in gain of body tissue or carcass composition between infection levels (Table 3.20). These results are surprising, since lesions in the intestinal tract were evident in all infected animals in experiment 2. Some leakage of protein into the gut in such circumstances might be expected (Charleston, 1976; Dargie, 1979), which may cause loss of plasma proteins and boost faecal nitrogen. This may be reflected in an increased demand for dietary protein and/or a reduction in protein deposition in the body. It may also be mistakenly taken to indicate a decrease in nitrogen digestibility because it is not normally possible to distinguish endogenous from exogenous nitrogen.

If this was the case, then the incremental demand for nitrogen was so small that it was not detectable, and there was sufficient surplus nitrogen supplied in the diet to cover losses.

Pattison et al (1980) identified lesions of oesophagostomiasis in intestinal tracts from infected pigs, and recorded a depression in apparent digestibility of nitrogen 29 to 38 days post-infection, but not earlier or later than this. However, nitrogen retention was not influenced by O.dentatum in their experiment, a similar result to the present study.

4.4 The Use of Dietary Energy

1 The maintenance requirement for metabolizable energy, ME_m

Maintenance values of ME (Table 3.13, Fig. 3.3) were derived by extrapolation to ER = 0 of the line derived from pigs fed at different energy intakes. This method has several shortcomings, the main criticisms being that it does not account for energy costs associated with mobilization of body fat nor nitrogen accretion at that point (Kielanowski, 1976; Fowler et al, 1979).

Regression equations of ER vs ME (Table 3.13) are shown for data unadjusted for treatment effects. The overall regression was significant ($t_{22} = 6.75$, $p < 0.01$), and the within-class regressions were homogeneous. The derived maintenance value, ME_m, for all pigs was 0.69 $MJ.kg.^{-0.66}day^{-1}$, which can be translated for comparative purposes to 0.49 $MJ.kg.^{-0.75}day^{-1}$. The maintenance value proved to be rather higher than previous values, 0.40 - 0.47 $MJ.kg.^{-0.75}day^{-1}$ arrived at in the same apparatus with gilts from the same source (Holmes et al, 1979). The maintenance requirement is slightly higher than other values derived for animals of a comparable liveweight (Table 4.3).

2 The efficiency of use of metabolizable energy for growth, Kg.

Mean values of energy retention are shown in Table 3.9a. There were no differences between infected and uninfected pigs for ER, ERF, ERP or ER/kgLWG in any balance period.

The value for k_g of 0.54 (using the liveweight base $W^{0.66}$, Table 3.13) which was recalculated to 0.55 (using the liveweight base $W^{0.75}$), was lower than that of 0.67 measured by Close (1978) at 25°C. The

Table 4.3 Estimates of the daily ME requirements of pigs for maintenance, 'a' in the equation $ME_m = aW^{0.75}$, for two sets of experiments, in those above the line the value was estimated as ME intake at zero energy balance. For those below the line the value was estimated from multiple regression equations incorporating P and F as independent variables (From: Fowler et al, 1979).

Body weight (kg)	a(MJ/day)	Source
2-6	0.542	Jordan and Brown (1970)
2-6	0.524	Jordan (1974)
13-30	0.455	Sharma, Young and Smith (1971)
13-30	0.570	Sharma, Young and Smith (1971)
20-30	0.522	McCracken and Gray (1972)
23-42	0.418	Verstegen et al (1973)
20-55	0.429-0.469	Verstegen and van der Hel (1974)
20-70	0.354-0.385	Holmes (1973)
20-70	0.418	Holmes (1974)
20-90	0.439	Fuller and Boyne (1972)
2.5-8.5	0.573	Kielanowski (1965)
5-21	0.601	Burlacu et al (1973)
20-90	0.473	Thorbek (1975)
8-15	0.682	Hoffmann et al (1977)
15-25	0.523	Hoffmann et al (1977)
25-35	0.561	Hoffmann et al (1977)
35-45	0.536	Hoffmann et al (1977)
23-42	0.511	Close, Verstegen and Mount (1973)
20-50	0.440	Close and Mount (1976; 1976a)
20-90	0.418	Kotarbinska (1969)
20-90	0.429	Houseman and McDonald (1973)
30-110	0.397	Gadeken, Oslage and Fliegel (1974)

value of 0.55 was also lower than values presented by Fuller and Boyne (1972) of 0.67 - 0.72 for pigs of 25-55 kg liveweight at 23°C, and rather lower than results presented by Holmes et al (1980) of 0.62 - 0.63 for gilts (see also Chapter 1, section 1.5.2).

3 The efficiency of use of metabolizable energy for fat deposition, k_f, and for protein deposition, k_p

The regression equations of ERF vs ME (Table 3.14) are shown for both infected and uninfected treatments and for the overall data, unadjusted for treatment effects. The overall regression was significant ($t_{22} = 6.12$, $p < 0.01$) and the within-class regressions were homogeneous. Therefore there was no influence of infection on the extent to which ME of the food was converted within the body into fat gain (Table 3.14).

Regression analysis of ERP vs ME resulted in only one significant relationship, that for uninfected pigs ($t_{10} = 3.65$, p 0.01; Table 3.15). Since the treatment equations were homogeneous with the pooled equations for both coefficients of $W^{0.66}$ and $W^{0.75}$, it was concluded that there was no association between ERP and ME for these pigs, 20 - 50 kg liveweight.

Multiple regression equations of ER with ME and NI, and ME with ERF and ERP were calculated using the liveweight base $W^{0.66}$. These showed no significant differences existed between infection treatments for the relationships between ER and ME or ER and NI (Table 3.17a), and no significant differences existed between infection treatments for the relationships between ME and ERF or ME and ERP (Table 3.18a).

The regressions in Table 3.17a show that ME exerted a large positive effect on ER, and NI exerted a small negative effect on ER. Both effects were highly significant. Holmes et al (1979), in

calculations using the exponent $W^{0.75}$ and using data from measurements from pigs of 30, 50 and 90 kg liveweight (Table 4.4), have shown similar results. For direct comparison with this and other work, the data in Table 3.17b was calculated using the liveweight base $W^{0.75}$.

The regressions in Table 3.18a give coefficients of 1.46 for ERF and 4.99 for ERP. For direct comparison with other work, Table 3.18b is presented using the liveweight base $W^{0.75}$, giving values of 1.45 ERF and 4.94 ERP. Holmes et al (1979) have shown a similar value of 1.44 ERF with gilts from 30 - 90 kg liveweight, but a much smaller value of 1.87 ERP with gilts 30 - 90 kg liveweight (Table 4.4). Similar levels of feed were offered in both experiments, so that the partition of ME between ERF and ERP would be expected to be similar. Differences in value for ERP were accounted for by the difference in the age of the animals in the two experiments and therefore the different rates of protein accretion. The rate of protein accretion is expected to be greater in animals of 25-55 kg LW than those 55 - 90 kg LW receiving an adequate nutrient supply (Whittemore, 1977). The standard error about the pooled coefficient for NE (4.99 ± 0.9) was larger in value than that of Holmes et al (1979; see Table 4.4) due partly to the narrow range in ERP (only a single level of crude protein was fed) in the present experiments.

4.5 The consequences of a difference in plane of nutrition

As expected, plane of nutrition exerted significant effects on several parameters of energy and nitrogen metabolism and performance (Tables 3.6a, 3.7a).

High-plane animals had significantly greater GE, FE, UE and ME

Table 4.4 Multiple regression equations for data pooled from measurements at 30, 50 and 90 kg LW (From: Holmes et al, 1979)

$ER = 0.66\ ME - 0.018\ NI - 0.276$ ($\pm$ 0.02) ($\pm$ 0.008)	$r = 0.98$
$ME = 1.44\ ERF + 1.87\ ERP + 0.46$ ($\pm$ 0.06) ($\pm$ 0.12)	$r = 0.99$

ER (MJ.kg.$^{-0.75}$day^{-1})

ME " "

ERF " "

ERP " "

NI (gms.kg.$^{-0.75}$day^{-1})

than their low-plane counterparts. The high-plane pigs also had significantly greater NI, FN, UN and NR than the low-plane pigs. In addition, high-plane pigs had significantly greater HP, ER, ERF and ERP than their low-plane counterparts. These comparisons were made collectively over all balance periods. These significant differences were attributable to the large difference in GE and NI, which were offered at 57% and 90% of appetite.

Plane of nutrition exerted a significant effect on HP, ER and ERF, but not on ERP, in separate analyses of balance periods (Tables 3.8a, 3.9a). Level of feeding also exerted a significantly different effect on UN in all analyses of separate balance periods. However, NR was significantly different only at the final balance period ($F_{1,3} = 11.5$, $p < 0.05$). The energy cost of protein deposition was estimated to be similar for both planes of nutrition (Table 3.18a).

Digestibilities of energy and nitrogen were the same for both planes of nutrition, (Tables 3.6a, 3.7a). Digestibility of energy in the ration (which contained 79% barley) varied between 76.85 and 77.98 $\pm$ 0.69. Holmes et al (1980) found energy digestibility figures for maize/barley rations to be 82% - 84%. One might expect a lower digestibility for the present ration which included a higher proportion of barley (Burlacu et al, 1978; Morgan et al, 1975a). Digestibility of nitrogen (77%) was close to values given by Holmes et al (1980) of 76% and 80%. Metabolizability of digestible energy was not significantly different between planes of nutrition; the pooled value of 96% was similar to values of 96% and 97% given by Holmes et al (1980).

CONCLUSIONS

CONCLUSIONS

Contrary to the findings of several independent studies that pig performance is adversely affected by infections with O.dentatum, the present study did not detect any effect of a single heavy artificial infection (80,000 larvae) with the parasite on performance, energy and nitrogen balance and carcass quality of growing pigs. This result was recorded at two planes of nutrition and in pigs housed individually or in groups. It is not known why the heavy worm burden was successfully tolerated by the pigs.

Possible reasons for detrimental effects having been recorded in the literature for some cases but not for others, may be the use of different strains of parasite and pig, and some unknown factor associated with the parasite (eg. bacterial invasion). Clearly this disagreement between results of different experiments, which has no obvious explanation, emphasizes a need for more detailed investigations of the pathophysiology of infection with O.dentatum. Possible areas for further study should include an attempt to identify other factor(s) necessary for achievement of significant effects, investigated with pigs given multiple infection, since single doses of larvae probably represent an artificial situation.

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APPENDICES

APPENDIX 1

Composition (percentage by weight) and calculated analysis of the grower diet

1. Composition

	Percentage
Barley meal	79.0
Pollard	5.0
Meat and bone meal	12.0
Blood meal	4.0
	100.0

A mineral/vitamin premix (Tasman Vaccine Laboratory, Auckland) was added to the diet at the rate of 2.5 kg/tonne. It supplied:

Vit A	9.0	m.i.u.
Vit D_3	1.0	m.i.u.
Vit E	20.000.0	i.u.
Vit K (menadione)	1.0	g
Vit B_1 (thiamine)	1.5	g
B_2 (riboflavin)	3.0	g
B_6 (pyriodoxine)	2.0	g
B_{12} (cyanocobalamin)	0.011	g
B_5 (pantothenic acid)	12.0	g
B_3 (niacin)	14.0	g
Choline	100.0	g
Iron	80.0	g
Zinc	150.0	g
Manganese	50.0	g
Copper	180.0	g
Iodine	2.0	g
Cobalt	0.3	g
Selenium	0.15	g
3 Nitro	25.0	g

m.i.u. = million international units.

i.u. = international units.

g = grams.

2. Calculated analysis (percentage fresh weight)

Apparent digestible energy (A.D.E.) 12.17 MJ/kg

	%
Crude protein (CP)	18.60
Lysine	0.90
Methionine/cystine	0.53
Tryptophan	0.23
Isoleucine	0.45
Calcium	1.36
Phosphorus	0.96

APPENDIX 2

Feeding Scales

Liveweight (kg)	Daily meal allowance (kg+) 90% appetite (High)	57% appetite (Low)
20.0	1.22	0.76
22.5	1.34	0.84
25	1.44	0.90
27.5	1.56	0.98
30	1.68	1.06
32.5	1.76	1.12
35	1.84	1.16
37.5	1.94	1.22
40	2.02	1.28
42.5	2.10	1.32
45	2.16	1.36
47.5	2.24	1.42
50	2.30	1.46
52.5	2.36	1.50
55	2.42	1.52
57.5	2.48	1.56
60	2.52	1.60
62.5	2.58	1.62
65	2.62	1.66
67.5	2.68	1.68
70	2.72	1.72
72.5	2.76	1.74
75	2.80	1.76
77.5	2.84	1.80
80	2.88	1.82

+Similar for entires and gilts.

APPENDIX 3

Calculation of heat production

from raw calorimetric data

Pig : 67

Date : 7/2/80

Atmospheric pressure : 757.9 mm

Cooler temperature : 10.6°C dew point

Meter-room temperature : 25.0°C

Measured air flow rate : 35.63 l/min

Flow through gas meters : 51308.54 l/day

Calorimeter volume : 2,200 litres.

Difference in O_2 concentration in calorimeter between the start and the finish of the measurement period

Oxygen (divisions)	Fresh air in	Exhaust air out	Difference
Start of measurement	10 (20.95%)	54 (19.65%)†	44 (1.30%)
End of measurement	15 (20.95%)	52 (19.70%)	37 (1.25%)

† The percentage oxygen values of the outgoing air were obtained by multiplying the appropriate $\%O_2$ per division figure by the number of divisions. The calculation of the percentage O_2 per division is shown below.

The number of chart divisions between incoming and outgoing O_2 (measured from spirometer aliquots) = 43.2 divs.

The number of chart divisions between incoming and outgoing CO_2 (measured from spirometer aliquots) = 55.9 divs.

Urinary nitrogen (g) = 10.73 (g/day)

Calibration of analyser with reference gases

Reference gas	O_2		CO_2	
	Known %	Reading in chart divs	Known %	Reading in chart divs
Bottle A	19.031	94.0	0.710	68.4
Bottle B	20.198	45.6	1.279	89.0

$(A-B)O_2$ = 48.4 divisions

O_2 per division = $\frac{1.167}{48.4}$ = 0.0241%O_2

Flow rate corrected to STP:

Correction factor = $\frac{757.9 - 9.3}{760}$ x $\frac{273}{273 + 25}$ = 0.902

Total ventilation rate:

Given 1440 minutes/day

average rate = (1440 x 35.63) l/day

= 51307.2

Correcting to S.T.P. = 51307.2 x 0.902 = 46301.3 l/day

Volume of Oxygen consumed:

1 chart division = 0.0241 % O_2

46.8 divisions = 43.2 x 0.0241 = 1.04

Volume of O_2 consumed = 46301.3 x $\frac{1.04}{100}$

= 478.00 litres/day

Correction for changes in components of air in calorimeter during the measurement period

Correction volume = -7 x 0.0241/100 x 2,200

= -4.05

Correcting volume of O_2 consumed = 482.05 - 4.05

= 478.00 l/day

Volume of CO_2 produced

Interpolating the value measured from the spirometer aliquot into the regression of the reference gases versus chart divisions, the 55.9 divisions corresponded to a percentage CO_2 reading of 1.175%.

Thus RQ = CO_2/O_2 = $1.175/1.041$ = 1.129

1.129 x corrected O_2 consumption = CO_2 consumption

= 1.129 x 478.00

= 539.47 l/min

Daily heat production

HP = (O_2 x 16.18) + (CO_2 x 5.02) + (N x 5.99) kJ.

HP = (478 x 16.18) + (539.47 x 5.02) + (10.73 x 5.99)

= 7734.04 + 2708.14 + 64.27

= 10377.91 kJ/day

= 10.38 MJ/day.

APPENDIX 4

Table 3.2b Test of homogeneity of the within-class (infection treatment, plane of nutrition) regression of $\log_{10}$ heat production (HP, $MJ.day^{-1}$) on $\log_{10}$ liveweight (LW, kg)

Source	df	MS	F	Level of significance
Main effects model	3			
Intra-class (infection treatment) regression of $\log_{10}$HP on $\log_{10}$LW	2	0.2111	521	**
Pooled within-class	1	0.4181	1030	**
Difference	1	0.0041	10.11	**
Residual error	18	0.0004		
Main effects model	3			
Intra-class (plane of nutrition) regression of $\log_{10}$HP on $\log_{10}$LW	2	0.2091	348.5	**
Pooled within-class	1	0.4181	697	**
Difference	1	0.0001	0.17	ns
Residual error	18	0.0006		

Table 3.3b Test of homogeneity of the within-class (infection treatment, plane of nutrition) regression of $\log_{10}$ nitrogen intake (NI, gms.day^{-1}) on $\log_{10}$ liveweight (LW, kg)

Source	df	MS	F	Level of significance
Main effects model	3			
Intra-class (infection treatment) regression of $\log_{10}$NI on $\log_{10}$LW	2	0.2098	29.97	**
Pooled within-class	1	0.4182	59.74	**
Difference	1	0.0013	0.18	ns
Residual error	18	0.007		
Main effects model	3			
Intra-class (plane of nutrition) regression of $\log_{10}$NI on $\log_{10}$LW	2	0.213	32.27	**
Pooled within-class	1	0.4182	63.36	**
Difference	1	0.0078	1.18	ns
Residual error	18	0.0066		

Table 3.4b Test of homogeneity of the within-class (infection treatment, plane of nutrition) regression of $\log_{10}$ metabolizable energy intake (ME, $MJ.day^{-1}$) on $\log_{10}$ liveweight (LW, kg)

Source	df	MS	F	Level of significance
Main effects model	3			
Intra-class (infection treatment) regression of $\log_{10}$ME on $\log_{10}$LW	2	0.222	29.75	**
Pooled within-class	1	0.439	62.7	**
Difference	1	0.0003	0.04	ns
Residual error	18	0.007		
Main effects model	3			
Intra-class (plane of nutrition) regression of $\log_{10}$ME on $\log_{10}$LW	2	0.2216	31.66	**
Pooled within-class	1	0.439	62.7	**
Difference	1	0.0046	0.66	ns
Residual error	18	0.007		

Table 3.5 Test of homogeneity of the within-class (infection treatment, plane of nutrition) regression of $\log_{10}$ energy retained (ER, $MJ.day^{-1}$) on $\log_{10}$ liveweight (LW,kg)

Source	df	MS	F	Level of significance
Main effects model	3			
Intra-class (infection treatment) regression of $\log_{10}$ER on $\log_{10}$LW	2	0.302	2.34	ns
Pooled within-class	1	0.528	4.09	ns
Difference	1	0.077	0.597	ns
Residual error	18	0.129		
Main effects model	3			
Intra-class (plane of nutrition) regression of $\log_{10}$ER on $\log_{10}$LW	2	0.298	2.29	ns
Pooled within-class	1	0.528	4.06	ns
Difference	1	0.069	0.53	ns
Residual error	18	0.13		

Table 3.6b Mean values of energy metabolism for pigs in experiment 1 ($MJ.kg^{-0.75}.day^{-1}$)

Variable	Infected	Uninfected	s.e.m.	Level of significance
Gross energy	1.56	1.55	± 0.01	**N
Faecal energy	0.35	0.35	± 0.01	**N
Urine energy	0.043	0.047	± 0.003	**N
Metabolizable energy	1.16	1.15	± 0.02	**N
Heat production	0.79	0.78	± 0.004	**N
Energy retained	0.37	0.37	± 0.02	**N
Energy retained as fat	0.31	0.31	± 0.02	**N
Energy retained as protein	0.057	0.054	± 0.004	**N

Table 3.7b Mean values of nitrogen metabolism for pigs in experiment 1 ($g.kg^{-0.75}.day^{-1}$)

Variable	Infected	Uninfected	s.e.m.	Level of significance
Nitrogen intake	3.05	3.05	± 0.05	**N
Faecal nitrogen	0.68	0.73	± 0.04	**N
Urinary nitrogen	0.85	0.88	± 0.04	**N
Nitrogen retained	1.52	1.43	± 0.09	**N
Mean liveweight ($kg^{0.75}$)	14.5	14.9	± 0.6	ns

Table 3.8b Mean values of several measurements of energy metabolism ($MJ.kg^{-0.75}.day^{-1}$)

Plane of nutrition	High		Low			Level of
Infection treatment	Infected	Uninfected	Infected	Uninfected	s.e.m.	signif.
Metabolizable energy intake						
Period 1	1.40	1.45	0.96	0.96	± 0.03	**N
2	1.44	1.42	0.89	0.86	± 0.06	**N
3	1.36	1.31	0.90	0.88	± 0.08	**N
Heat production						
Period 1	0.91	0.94	0.65	0.67	± 0.006	**I**N
2	0.91	0.89	0.68	0.67	± 0.02	**N
3	0.89	0.88	0.67	0.63	± 0.03	*N

Table 3.9b Mean values of several measurements of energy retained ($MJ.kg^{-0.75}.day$)

Plane of nutrition	High		Low			Level of
Infection treatment	Infected	Uninfected	Infected	Uninfected	s.e.m.	significance
Energy retained						
Period 1	0.49	0.51	0.29	0.29	± 0.02	**N
2	0.53	0.52	0.20	0.19	± 0.05	**N
3	0.47	0.44	0.23	0.24	± 0.08	*N
Energy retained as fat						
Period 1	0.42	0.44	0.25	0.24	± 0.01	**N
2	0.47	0.47	0.15	0.15	± 0.06	**N
3	0.39	0.37	0.19	0.20	± 0.06	*N
Energy retained as protein						
Period 1	0.069	0.070	0.043	0.043	± 0.01	*N
2	0.064	0.059	0.053	0.046	± 0.01	ns
3	0.075	0.069	0.041	0.038	± 0.01	*N

Table 3.10b Mean values of several measurements of nitrogen metabolism ($g.kg^{-0.75}.day^{-1}$)

Plane of nutrition	High		Low			Level of
Infection treatment	Infected	Uninfected	Infected	Uninfected	s.e.m.	significance
Nitrogen intake						
Period 1	3.69	3.81	2.39	2.42	± 0.3	**N
2	3.56	3.46	2.59	2.54	± 0.2	**N
3	3.82	3.81	2.30	2.28	± 0.3	**N
Urinary N excreted						
Period 1	0.95	0.97	0.78	0.75	± 0.05	**N
2	0.94	0.89	0.64	0.76	± 0.08	*N
3	1.11	1.13	0.73	0.79	± 0.15	*N
N retained						
Period 1	1.82	1.82	1.14	1.15	± 0.3	ns
2	1.69	1.57	1.39	1.22	± 0.3	ns
3	1.98	1.81	1.08	1.01	± 0.4	*N

Table 3.16b Test of homogeneity of the within-class (infection treatment, plane of nutrition) regression of energy retained as protein (ERP, $MJ.kg^{-0.66}.day^{-1}$) on nitrogen intake (NI, $g.kg^{-0.66}.day^{-1}$)

Source	df	MS	F	Level of significance
Main effects model	3			
Intra-class (infection treatment) regression of ERP on NI	2	0.002	44	**
Pooled within-class	1	0.0039	87	**
Difference	1	0.00005	1.1	ns
Residual error	18	0.00005		
Main effects model	3			
Intra-class (plane of nutrition) regression of ERP on NI	2	0.0021	4.8	*
Pooled within-class	1	0.0039	91	**
Difference	1	0.00015	3.46	ns
Residual error	18	0.00004		

Table 3.17b Multiple regression equations relating energy retained (ER, $MJ.kg^{-0.75}.day^{-1}$) to metabolizable energy intake (ME, $MJ.kg^{-0.75}.day^{-1}$) and nitrogen intake (NI, $MJ.kg^{-0.75}.day^{-1}$)

Source of data	Regression equations
Infected	$ER = 0.77\ ME^{**} - 0.08\ NI^{*} - 0.27$ ($\pm$ 0.09) ($\pm$ 0.03)
Uninfected	$ER = 0.76\ ME^{**} - 0.09\ NI^{*} - 0.21$ ($\pm$ 0.07) ($\pm$ 0.03)
Pooled within-class (infection, nutrition)	$ER = 0.76\ ME^{**} - 0.09\ NI^{**} - 0.24$ ($\pm$ 0.06) ($\pm$ 0.02)

ME, NI : r = 0.88

Table 3.18b Multiple regression equations relating metabolizable energy intake (ME, $MJ.kg^{-0.75}.day^{-1}$) to energy retained as fat (ERF, $MJ.kg^{-0.75}.day^{-1}$) and as protein (ERP, $MJ.kg^{-0.75}.day^{-1}$)

Source of data	Regression equations
Infected	$ME = 1.42\ ERF^{**} (\pm 0.16) + 4.48\ ERP^{**} (\pm 1.41) + 0.46$
Uninfected	$ME = 1.50\ ERF^{**} (\pm 0.12) + 5.50\ ERP^{**} (\pm 1.07) + 0.38$
Pooled within-class (infection, nutrition)	$ME = 1.45\ ERF^{**} (\pm 0.09) + 4.94\ ERP^{**} (\pm 0.83) + 0.43$

ERF, ERP: $r = 0.40$

APPENDIX 5

Maximum faecal egg counts (epg) and estimated total worm numbers recovered from pigs in Experiment 2

Pig No.	Maximum egg count	Estimated number of worms at slaughter
1	29,750	6,850
2	15,625	6,300
3	36,250	9,200
4	17,575	4,050
5	32,125	4,750
6	17,875	2,550
7	11,825	3,900
8	28,500	2,000
9	25,825	1,950
10	25,400	7,500
11	2,825	70
12	9,400	1,800
13	16,475	4,300
14	9,250	4,350

The relationship between maximum egg counts and numbers of worms at slaughter, $r = 0.59$.

ADDENDUM

ADDENDUM

Since going to print, a further study with Oesophagostomum spp. has been published.

In two experiments, Hale et al (1981) artificially infected growing-finishing pigs with doses composed of O.quadrispinulatum and O.dentatum in a ratio of about 3 to 1. Single dose infections were administered with varying numbers of infective larvae.

In the first experiment, at 21 days post-infection, uninfected pigs had gained weight 11% faster and required less feed per unit of liveweight gain than pigs given either 1,100 larvae/kg bodyweight or 1,650 larvae/kg bodyweight. However, after 77 days post-infection, final liveweight, average daily gain and feed consumed were not significantly altered by infection. The results of Hale et al (1981) show significant effects to day 21 post-infection which were not recorded in the present study. The overall result of the work of Hale et al (1981) agrees with the present study, but not with results of Pattison et al (1980). In experiment 2 Hale et al (1981) found uninfected pigs had higher digestion coefficients for dry matter ($p < 0.01$), ash ($p < 0.05$), crude fiber ($p < 0.01$) and nitrogen free extract (NFE) than did pigs infected with nodular worms. This result agrees with Pattison et al (1980) and Pattison and Thomas (1976), but not with the present study.

These more recent experiments highlight the need for work to proceed beyond performance and digestibility trials, to work which will elucidate the relationship between host and parasite and identify factor(s) which produce the recorded disagreement in findings.