THE ENERGY METABOLISM OF YOUNG FRIESIAN CALVES FED ON A DIET CONSISTING OF MILK AND MEAL

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ABSTRACT

Two Friesian bull calves were selected from those born each week for six weeks during March and April 1975. The twelve calves were used in an experiment to study the energy metabolism of young calves when fed a milk and meal diet.

1. All calves were reared on fresh whole milk with pelleted concentrate available ad lib. Between 21 and 42 days of age intake was adjusted so that each animal received half of its daily allowance of ME from milk and half from meal. From each pair, one calf was assigned randomly to a high level, and its pair mate consequently to a low level of feeding.

2. Energy and nitrogen balances (seven days duration) were measured once for all pairs of calves and twice for the last three pairs.

3. Heat production (MJ/day) was related to liveweight (kg) by $HP = .200\ LW^{.980}$, and metabolizable energy to liveweight by $ME = .340\ LW^{.922}$.

4. The data for heat production, metabolizable energy intake and energy retention were interpreted to provide estimates of 'true' net energy required for maintenance of 0.26 $MJ/kg^{0.75}$ daily.

5. The pooled values for ME required for maintenance were 0.37 and 0.41 MJ $ME/kg^{0.75}$ daily determined by simple and multiple regression techniques respectively. The net efficiency of utilization of ME above maintenance was 0.63 determined by simple regression.

6. Pooled values for the partial net efficiencies of utilization of ME for the synthesis of protein and fat were 0.38 and 1.00 respectively.

7. ME required above maintenance per kg of liveweight gain was 16.53 and 12.85 for the high and low feeding levels respectively. The difference between these values was not significant and the pooled value was 14.89 MJ ME/kg liveweight gain.

8. Methane losses accounted for less than 2% of GE. The metabolizability (ME/GE) of the combined diet was 78% and DE/ME 0.94.

9. Obligatory losses of N were 0.19 $gN/d/kg^{0.75}$, N maintenance (N_m) was 0.35 $gN/kg^{0.75}$ daily, the digestibility was 81% and the biological value 0.53.

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CHAPTER 1

INTRODUCTION

The energy requirements of the pre-ruminant calf were reviewed by Davey (1974), who drew attention to the considerable variation between the estimates of various workers of the metabolizable energy (ME) required for maintenance, energy costs per unit liveweight gain and efficiencies of utilization of ME above maintenance. Holmes and Davey (1976) subsequently confirmed the much lower estimates of recent workers; Vermorel, Bouvier, Thivend and Toullec (1974); Van Es, Nijkamp, Van Weerden and Van Hellemond (1969) and Johnson and Elliot (1972a, b). Estimates of the energy requirements of ruminant calves have been studied by many workers including Neergaard (1974) and Blaxter, Clapperton and Wainman (1966) and these estimates are considerably higher for maintenance and energy costs per unit liveweight gain than for pre-ruminant calves.

However for calves fed on a diet of milk and concentrate little information is available on the estimates for maintenance, energy costs of liveweight gain or net efficiencies. The following work was carried out for this reason and also to investigate whether the change in efficiency from pre-ruminant to ruminant is a sudden one.

The review of literature begins with a brief outline of the anatomical and physiological development of the rumen. This describes variations in the stages of rumen development, the changes in the nature of the end-products of the rumen digestive process, the ability of the animal to absorb the end-products of digestion and the energy costs of digestion when compared to that of a pre-ruminant. Following this a hypothetical model which attempts to integrate factors controlling voluntary feed intake in the young calf is introduced. Emphasis is given in this Section to factors which modify intake which ultimately effect the energy and nitrogen balance of the animal. The final section covers briefly the importance of techniques used in estimating

measurements of energy and nitrogen metabolism in the young calf. Estimates of these measures, from reported studies, are presented at the conclusion of this Section.

CHAPTER 2

REVIEW OF LITERATURE

I. ANATOMICAL AND PHYSIOLOGICAL DEVELOPMENT OF THE RUMINANT CALF

Introduction

Although the calf begins life with its stomach already divided into the four compartments characteristic of the adult ruminant, the relative sizes of these are quite different from those in the mature animal. The ruminant is a symbiotic relationship between animal and micro organisms which evolved to enable the animal to live on high fibre diets. The animal provides the rumen organisms with the following facilities: a large fermentation vessel, gathering and selection of substrate, maceration and mixing of food, temperature control, pH control through the buffering action of saliva especially, provision of extra nutrients; (e.g. urea and phosphates in the saliva or through the rumen wall) removal of inhibitory products and removal of indigestible solids.

Mature ruminants are assumed to have the same basic nutritional requirements for energy, amino acids, vitamins, minerals and water as do the simple stomached animals. Their digestive juices, like all other animals, lack cellulases and a diverse population of micro organisms located largely within the rumen and to a lesser extent in the caecum and colon, enables them to thrive on fibrous plant feeds that are frequently deficient in some of the essential amino acids and water soluble vitamins.

Only a small proportion of dietary nutrients survive the microbial activity of the rumen. Dietary protein introduced to the rumen is largely hydrolyzed into amino acids, short chain fatty acids and ammonia. These degradation products together with NPN compounds of the feed and saliva are then resynthesized into bacterial and protozoal proteins. These reconstituted proteinsundergo normal gastric digestion in the abomasum along with liquid fed protein which by-passed the rumen via the oesophageal groove and absorption may take place in the distal portions of the alimentary tract. Other rumen fermentation end products are volatile fatty acids (V.F.A.) and the various vitamins. The V.F.A's. are absorbed directly from the rumen and serve as the major source of energy in ruminants (Carrol and Hungate, 1954; Balch, 1958; Blaxter, 1962).

Anatomical Development

The rumen in calves at birth is small undeveloped and is tucked away in the anterior-dorsal aspect of the abdominal cavity (Tamate, McGilliard, Jacobson and Getty, 1962; Sisson and Grossman, 1953). Rumen volume varies from 0.5 → 1.6 l., and represents approximately one third of the total stomach capacity (Warner, Flatt and Loosli, 1956; Tamate et al., 1962). The rumen wall is thin and the papillae on its inner surface are short and undeveloped (Warner et al., 1956; Tamate et al., 1962). The age at which transition to the ruminant method of digestion occurs is largely dependent on the diet that a calf receives (Preston, 1963). Table 2.1, from Church (1970) outlining changes in rumen development of calves with age, fed the following diet (milk, concentrate, hay) demonstrates this point.

TABLE 2.1 Percentage of bovine stomach tissue contributed by each compartment.

Compartment	Age in weeks						Source
	0	4	8	12	16	20-26	Becker & Arnold (1952)
Reticulo Rumen	38	52	60	64	64	64	Godfrey (1961)
Omasum	13	12	13	14	22	25	Tamate et al. (1962)
Abomasum	49	36	27	22	15	11	Warner et al. (1956)

The capacity of the reticulorumen and the total stomach at 12 weeks was about twice as large for calves fed milk, hay and grain as for those receiving only milk (Tamate et al., 1962). The reticulorumen of milk fed animals at this age apart from being smaller, are thinner walled, and lack papillary development. If the diet is confined to natural or artificial milk, all the stomach compartments grow in weight and size at the same rate as that of the whole body (Warner et al., 1956). Under these conditions only the abomasum may be functional. On the introduction of dry feeds the pattern of development is quite different. The abomasum continues to develop at the same rate as when only milk is given, but the other compartments grow more rapidly (Warner et al., 1956). The presence of inert mass such as shavings, sawdust or sponges in the reticulorumen has resulted in an increased growth of rumen musculature (Harrison et al., 1960) and capacity (Warner, 1961) compared with calves fed only milk. From reviewing several studies Warner and Flatt (1964) concluded that the reticulorumen volume of calves on a hay grain ration reaches its adult proportions per kg. of ingesta

free body weight by 12 to 16 weeks, but the omasum keeps growing (relative to body size) until about one year.

Papillary Growth

At birth reticulorumen papillae are less than 1mm in height but on the introduction of solid food grow rapidly to their maximum length (Tamate et al., 1962; Tamate et al., 1964; Warner et al., 1956). Inert materials such as sponges sawdust or shavings as well as milk have failed to cause papillae elongation (Flatt et al., 1958; Tamate et al., 1962). Brownless (1956) and Warner et al., (1956) observed a high degree of papillary development in calves fed on high concentrate low fibre diets and suggested that the products of rumen fermentation act as the primary stimuli for rumen development. This hypothesis has since been confirmed and the active principles identified as the VFA's (Flatt, Warner and Loosli, 1959; Tamate et al., 1962). Infusion studies of volatile fatty acid (V.F.A.) salts (reviewed Preston 1963) established an order of effectiveness, butyrate propionate acetate. The experiments of Harrison, Warner, Sander and Loosli (1960) further indicate a regression of rumen papillae in calves that were changed from a diet containing hay and concentrates to one that was composed of milk only, thus indicating that active fermentation was essential for maintenance of rumen papillae. A period of three weeks is sufficient for increased papillary development to occur in calves transferred from a high roughage diet to one of all concentrates, and for atrophy of papillae if transferred from a high concentrate diet to one of all hay (Stobo et al., 1966).

Comparisons of high or low roughage diets in the rearing period from 4 months to 2 years of age showed no effect of the method of rearing on the ability of the heifers to digest hay or mixed rations of hay and concentrates (Balch et al., 1960) despite possible differences in papillae length.

Excessive papillary development which may occur on highly fermentable low fibre concentrates may lead to parakeratosis, a condition where papillae increase in length, clump and become encrusted with a keratinized material which may reduce their absorptive effectiveness (Bull et al., 1965; Garret et al., 1961).

Development of rumen microorganism populations

Right from the first days of life small quantities of milk pass into the rumen and the appropriate substrate microorganisms immediately begin to develop (Ziolecki and Briggs, 1961). Mann and Oxford (1955) found the abomasum to support a large diverse population of lacto-bacilli which may innoculate the rumen through back flow. Lengman and Allen (1959) working with milk fed calves reported bacteria numbers remaining low but these increased when solid feeds were given, (Bryant and Small, 1956) and those protozoa which were present after milk alone diets; disappeared on ad. lib. concentrate feeding. Protozoa especially the ciliates failed to effectively establish unless contact was made with other animals (Bryant and Small, 1956) and even then only survived on mainly roughage diets until about 5 months of life (Eadie et al., 1959). An excellent review of rumen protozoal development, classification, and characteristics in the young ruminant is presented by Barnett and Reid (1961). Lactobacilli numbers were enhanced under concentrate feeding but diminished under high levels of roughage feeding, and

the inverse relationship between ciliates and lactobacilli is thought to be mainly due to rumen pH. (Eadie et al., 1967). Since cud innoculation from mature animals has been established to develop the adult type rumen population in calves (Hibbs et al., 1953) numerous attempts have been made to see whether this results in more rapidly growing animals. Critical evaluation of the reported experiments indicates that it is not so much innoculation as the type of diet given which governs the species of flora and fauna which appear in the rumen (Preston, 1958; Eadie et al., 1959) Nevertheless innoculation of one sort or another is definitely required for rumen microbial growth.

Physiological Development

Before rumen development the efficient use of liquid food depends on whether the animal possesses the appropriate enzymes (Radostits and Bell, 1971 Review), while the utilization of solid foods depends on the degree of development of the rumen and its microorganisms (Preston, 1963). By measuring cellulose digestion McCarthy and Kesley (1956) and Stewart (1962) found ruminal type fermentation to exist at 3 weeks of age. Stewart (1962) suggested fermentation similar to adults began at 2 weeks of age but development was hindered by lack of sufficient substrate. These results are in general agreement with those of Godfrey (1961) and Lengemann and Allen (1959).

Khouri (1966) disagreeing with Sutton et al., 1963 found ruminal mucosa was capable of assimilating and utilizing acetate -1-C^{14} within a week of birth. He concluded from his work that since calves were capable of absorbing VFA's from the rumen and utilizing them during the first week of postnatal life, prior to

the consumption of solid feeds and establishment of a rumen microbial fermentation similar to adult animals, then the increased capacity to absorb VFA's accompanying rumen development (Huber, 1975) was dependent on the expansion of pre-existing mechanisms rather than the development of new ones. Calves on a solid feed intake have ruminal VFA concentrations similar to adults when fed on solid, at 6-8 weeks (Hibbs et al., 1956; Huber, 1975).

Hexoses, the predominant energy supply in the preruminant, are absorbed mainly in the small intestine while VFA's are absorbed mainly in the reticulorumen. Hence on rumen development sites of digestion and absorption change as does blood glucose level, glucose tolerance, glucose utilization rate and gluconeogenesis (Edward, 1970).

Leibholz (1975) studied rumen development in Friesian calves given milk for 5 weeks then weaned onto a mainly barley diet. Of the DM (dry matter) ingested 76% was recovered at the duodenum one week after weaning, 58% two weeks after and 46% the adult level (Sharma et al., 1974) at 8 weeks after weaning. The digestion of acid detergent fibre also reached adult levels by 8 weeks post weaning. The flow of nitrogen to the duodenum was similar to intake of N which was the same as found for the pre-ruminant calf (Leibholz, 1975). In the first week after weaning, 32% of the nitrogen flowing to the duodenum was of microbial origin, this increased to 74% by 7 weeks after weaning.

In this study the rate of microbial protein synthesized per 100g of organic matter reached adult levels as reported by Hogan and Weston (1967), Smith, (1974) and Hume (1970) within a week of weaning. This work of Leibholz (1975) gives some idea of the rate at which the digestive system of the recently weaned calf approaches adult status.

II. FACTORS AFFECTING VOLUNTARY INTAKE AND THE DEVELOPMENT OF SOLID FEED INTAKE IN YOUNG CALVES

The amount of food consumed by animals largely determines their productive output, and an understanding of how they regulate voluntary food intake (V.F.I.) is of fundamental importance in the field of animal nutrition.

The factors controlling food intake are complex and are not fully understood (Baile and Forbes (1974). The multifactorial nature of voluntary food intake presents many problems as experiments aimed at eliminating one control, in an attempt to understand the system, have often shown that the eliminated control is dispensable and that other control mechanisms are invoked to maintain food intake (Davey, 1975).

Two important concepts relating to voluntary intake in ruminants are summarized in a model proposed by Montgomery and Baumgardt (1965c) - see Fig. 2.1

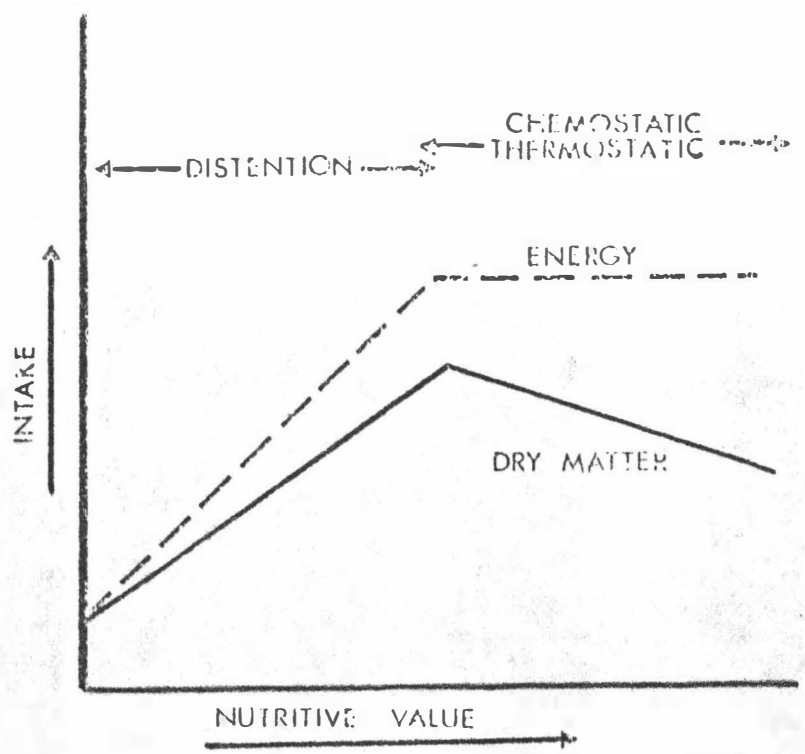


FIGURE 2.1 Probable relationships between energy and food intake and controlling mechanisms. From Montgomery and Baumgardt (1965a)

The first concept involves the extent by which the alimentary tract can accommodate food residues and is represented in Fig. 2.1 by the portion under the distention side. The distention portion of the model represents that portion of VFI under "physical" control and has been reviewed by Balch and Campling, 1962; Campling, 1970 and Conrad, 1966. The chemostatic-thermostatic portion of the model represents the extent to which absorbed nutrients control intake -"metabolic" control. This method of control has been reviewed by Baile and Meyer (1970) and Baumgardt (1970). Thus in a simplified summary animals receiving a diet of high caloric density are able to consume enough DM to satisfy their physiological demands for energy where with low caloric density diets gut load may prevent it. This type of relationship has been suggested by Owen et al. 1969, Andrew, Ray and Ørskov 1969, Andrews and Ørskov 1970, Kay, McLeod and Andrew 1972, Kang and Keibholz 1973, Byford 1974).

The voluntary feed intake in young ruminants will be dealt with under two headings:

1. Diets the intake of which is possibly controlled by physical means
2. Diets the intake of which is probably controlled by metabolic means

It must be stressed that this division is arbitrary and control by either means are not independent, e.g. Egan (1970) states that a complex of interacting physical and metabolic factors may be involved throughout the whole range of diets utilized by ruminants and that there is not simply a switch over to metabolic regulation at a point where disposal of indigestible bulk is no longer an embarassment or limitation to total digestible energy intake.

2.1.1 PHYSICAL MEANS OF CONTROL

The development of the reticulorumen with age (Warner and Flatt, 1965; Hodgson, 1971c) has been suggested as an explanation (Andrews et al., 1969) for the greater ability of the young ruminant with increasing age to equalize intakes of digestible energy from diets of different energy density as has been shown by Owen et al., 1969; Andrews et al., 1969; Andrews and Ørskov (1970)working with lambs and McCullough (1969) with calves. In these experiments the energy concentration of the diet was altered by altering the concentrate to hay ratio and the most pronounced effects of age were when the hay was left unground. This suggests the young ruminant shortly after weaning has not sufficient rumen volume or rate of passage. Rumen distention appears as a prominent satiety signal in controlling intake in older ruminants also (see review Baile and Forbes, 1974). Up to now evidence is only circumstantial with the problem being in the separation and interpretation of the role of rumen development in the development of intake of solid food in young ruminants as the pattern of the development of these two factors are similar (Hodgson, 1965; Warner and Flatt, 1965).

Therefore although Hodgson (1971c) and (1973) was able to demonstrate a significant relationship between DM intake and weight of digesta in the rumen over this transitional period of the calf's life such a relationship does not clarify cause and effect.

It was demonstrated (Hodgson, 1965, 1971a, b) that the initial development of intake of solids was related to an increase in time spent eating but later increases in intake were achieved by greater DM uptake per unit time spent eating with no increase in eating time.

These results support the work of Swanson and Harris (1958) and later work by Byford (1974) may also be interpreted this way.

Hodgson postulated that the initial development of solid food intake in the young ruminant may be limited primarily by behavioural factors (Hodgson, 1971a), and that gut development was dependent on the intake of solid foods and not the reverse (Hodgson, 1971c).

Hodgson (1971a) using rumen fistula's and adding and removing digesta, demonstrated that calves were unable to compensate in either a positive or negative way in a food consumption sense, however responses approached adult levels six weeks post weaning. Hodgson concluded that the intake of solid foods shortly after weaning was limited primarily by oropharyngeal factors and rumen development was postulated as dependent on the intake of solid foods. Further possible indirect evidence is that the response to sweetening agents is greater in young ruminants (Preston, 1956; Gardner, 1967) than older animals (Balch and Campling, 1962) which might be expected if behavioural factors are of importance. Exhaustion of salivary glands (Kellaway, Grant and Chudleigh, 1973b) has also been found to be an important factor in influencing intake in early weaned ruminants. The work of Byford (1974) feeding concentrates or pasture to early weaned calves also supports this hypothesis of Hodgsons.

It would appear that the importance of oropharyngeal based mechanisms are transient, as their importance in mature ruminants has been discounted (Balch and Campling, 1962). As Hodgson's (1971d) and (1973) work was based solely on work with dried grass of moderate to low quality (in vivo digestibility 52-57%) as a solid food and

live weight gain (LWG) of the calves was only of the order of .3 kg/day it may be possible with diets of higher energy density that an animal's demand for energy may be satisfied within the limits imposed by rumen capacity or oropharyngeal factors.

2.1.2. METABOLIC MEANS OF CONTROL

The validity of the relationship between intake and nutritive value as described by Montgomery and Baumgardt (1965a) in Fig. 2.1 may be questioned on two points.

1. When an animal's intake is being controlled by its demand for energy then theoretically it should be performing at a level close to its genetic potential. In the experiments of Kay et al., 1970, 1972; Kang and Leibholz, 1973; Byford, 1974, where calves were weaned at five weeks of age and fed diets of varying energy concentrations ad lib. the maximum growth rate of the calves was approaching the order of 0.8kg/day. However Friesian calves of a similar age over a similar time span grew at up to 1.5kg/day (Van Es, 1969; Roy, 1964, 1975). This would suggest factors other than physiological demand for energy were controlling the intake of these concentrate diets in the early weaned calf.

2. Because growth rates were similar for diets of differing energy density, could this confirm that animals ate to maintain a prescribed metabolizable energy intake? Conclusions based on liveweight gain information from diets of differing fibre levels can easily be misinterpreted because of differences in amounts of digestive tract fill (Stobo and Roy, 1963; Johnson, 1972; Jahn, Chandler and Polan, 1970; Strozinsky and Chandler, 1971). More recent work by McCullough (1974) found DM intake was affected by fibre level and that the changes in digestion and utilization of energy accounted for the similar liveweight gains measured.

These two criticisms do not unequivocally disprove the existence of a homeostatic mechanism operating to maintain a prescribed intake of energy by young ruminants but they do raise doubts. In an attempt to substantiate these doubts an alternative explanation as to why this relationship between nutritive value and intake occurs in early weaned ruminants is given below.

The levelling off, or even in some cases (Kay et al., 1970) the falling off of D.E. intake of early weaned ruminants with further increases in the D.E. concentration of the diet may be related to decreases in rumen pH associated with the intake of these types of diets (Bhattacharya and Warner, 1967). The feeding of high grain diets to ruminants can result in lactic acidosis (Kellaway et al., 1973b) which impairs rumen motility, may lead to bloat, and is generally associated with anorexia (Scarisbrick, 1954). Kay, Fell and Boyne (1969) have shown that pathological changes take place in the rumen wall (rumenitis) when the pH of the rumen contents fall below pH 5.6. While Andrews et al (1969) and Kay (1969) have shown that when early weaned lambs and calves are fed concentrate ad. lib. rumen pH is below 5.5. Battacharya and Warner (1967) have demonstrated a corresponding drop in intake with a drop in pH, but whether this response to pH was monitored as such in the voluntary feed intake centre or the centre responded to some other factor is unknown, especially when the later work of Chase and Wangness (1975) is considered. Working with both sheep and calves fed high energy rations they established that rapid physiological changes do occur in response to meal initiation and during the meal but no cause and effect relationship was found between a metabolite and the control of the meal size.

One of the main reasons for a drop in rumen pH on high energy concentrate diets is a decrease in salivary buffering brought about by a lowering of both total salivary secretion and buffering capacity of saliva because of the low rumination times on concentrates (Oltzen, Pullman and Davies, 1965). Restoration of rumen pH to normal levels and thus increases in intake of diets of high D.E. concentration can be brought about by the inclusion of fibre (Preston, 1963; Leibholz, 1975) or inclusion of buffers (Preston et al., 1961, Kang and Leibholz, 1973). Fibre has its effect in two ways, firstly as a supplier of basic cations (Matrone, Ramsey and Wise, 1969) and secondly by stimulating salivary secretion (Weis, 1953 cited by Preston, 1963). Kellaway et al., 1973a) found the later function of roughages was the more important of the two. While Leibholz (1975) found roughage alone was sufficient to produce rapid growth rates in recently weaned calves, Kellaway et al. (1973b)found their calves required both buffers and roughage to obtain the best results. The growth rates recorded by Kellaway et al., (1973b) and Leibholz (1975) approach those of Roy (1964, 1975) for liquid fed calves which may indicate that once the deficiency of the buffering capacity of the early weaned ruminant is overcome, it may grow at rates near its genetic potential.

The overall conclusion is that intake of solid food by early weaned ruminants may be controlled to a large extent by oropharyngeal based mechanisms and that young ruminants need time to become adapted to solid food.

2.1.3. Factors influencing the development of solid food intake in young ruminants

Factors of possible importance here could be: birth weight, sex of animal, milk feeding regime and characteristic of solid food.

Birth Weight

Birth weight varies with breed (Preston and Willis, 1974), the belief among farmers being that growth rate of lighter calves is slower and mortality higher than for heavy calves. Kay (1969) examining the records of 150 Friesian bull calves with varying birth weights found birthweight to have no effect on subsequent growth to weaning at 100kg. Results from other work, e.g. Leaver and Yarrow (1972) are confounded because of their constant feed allowance irrespective of liveweight as Davey (1974) showed that allowances based on percentage liveweight will in some cases underfeed the lighter calves relative to the heavier ones.

Sex

Comparisons between male and female calves (Armstrong, 1966) suggest sex had no effect initially on the development of solid feed intake.

Milk feeding regime

This is dealt with under the following three headings:

1. Direct effect of the level of milk fed.
2. Age of animal at weaning.
3. Carryover effect of the preweaning treatment on the intake of solid food post-weaning.

1. Direct effect of the level of milk fed

An inverse relationship between the level of milk fed and the intake of solid food in young ruminant calves has been demonstrated by many workers (Mathieu and Wegat'Litre, 1961; Burt and Bell, 1962; Armstrong, 1966; Tayler, 1966; Hodgson, 1971c and Leaver and Yarrow (1972).

$$Y = b\frac{1}{X} + c \qquad (1)$$

Y = intake of solids (g DM/kg LW)

X = intake of milk, the level of milk fed (g DM/kg LW)

b = regression coefficient

c = a residual term.

Hodgson (1971c) quantified the above mentioned inverse relationship with calves fed grass and found the regression coefficient (the ability of the calf to substitute solid food for a given change in milk intake) was significant and increased with age. This could represent the cumulative effects of low levels of milk feeding as the calf ages, on the intake of solid food (Mathieu and Wegat-Litre, 1961) but because the regression increased with age independent of the fluctuations in milk feeding (Spedding et al., 1963) Hodgson (1971c) proposed that the response was one of adaption to a solid diet (see earlier section on rumen development). Obviously the value of the regression coefficient is going to alter according to the type and form of the solid diet (Hodgson, 1971a). The increase with age of the regression coefficient would seem to suggest some advantage in feeding calves a greater level of the fixed quantity of milk to be fed before weaning when they were young and consequently had a very low substitution rate for solids. However the limited work with lambs and calves (Preston, 1956; Quayle, 1958 and Owen et al., 1969) would not support this suggestion as the pattern of distribution of a fixed quantity of milk over a set time period had little effect on performance. It would appear the performance of milk fed ruminants is insensitive to the distribution of milk feeding, but is sensitive to the level of milk fed. The last point will receive greater coverage at a later stage.

2. The age of the animal at weaning

Checks in liveweight gain at weaning in regard to age have been observed by Converse (1949); Stobo, Roy and Gaston (1967a) and Hodgson (1965), the check generally being greatest in the younger calves. Hodgson (1965) and Stobo et al. (1967) showed that this was the result of a slower rate of increase in the intake of solid food post-weaning with the younger animals, reflecting the lower extent of the substitution of solid food for milk at the younger age (Hodgson, 1971c). Part of this effect may be due to age per se although age at weaning is often a reflection of a number of other variables which may or may not be related to the development of the intake of solid food post-weaning.

3. Carryover effect on the pre-weaning treatment on the intake of solid food post-weaning

Since the early work of Preston (1957) was published the general trend with calves to be weaned at an early age was to encourage them to eat as much solid food as possible before weaning. However the literature is not clear in regard to the quantitative importance of the intake of solid food pre-weaning as it effects the intake of solid food post-weaning. The confusion can be reconciled to some extent by considering the relationship between the intake of solid food before and after weaning in two categories.

(i) When comparisons are made between individual animals reared on the same treatment - only one treatment with the same allowances of milk and solids before weaning. Most confusion seems to arise over this point as workers have produced conflicting results. Quayle (1958) cited by Hodgson (1965) showed the relationship between intake of solid food by calves before and after weaning was not close.

Davies and Owen (1967) feeding lambs on a restricted supply of milk agreed with Quayle (1958) but when milk was fed ad lib. in the same experiment to another group of lambs a close positive relationship was established between the intake of solid food before and after weaning. This contradiction is not strictly related to the amount of milk fed as Lawrence and Pearce (1965) when feeding calves a restricted milk ration obtained a highly significant positive relationship between intake of concentrates before and after weaning.

(ii) When comparisons are made between different groups of animals receiving different levels of milk and weaned at the same age. Again a certain amount of confusion is evident. Hussian (1963) cited by Hodgson (1971), Davies and Owen, (1967) and Hodgson, (1971) have consistently shown that with groups of animals receiving different quantities of milk and weaned at the same age, the regression of DM intake after weaning on milk intake before weaning was significantly negative and persisted for some time. However Brookes and Davey (1975) feeding three levels of whole milk, weaned their calves at 55 days and found the regression of DE intake of a concentrate hay diet on DE intake of milk was not significant. This indicated that animals restricted before weaning did not respond by increasing their DE intake of concentrate hay when this was offered ad libitum after weaning. The reason for the persistence of the difference established in the intake of solid food before weaning in the post weaning period (Hodgson, 1971) is not clear although it could be due to a greater rumen development because the calves had eaten more solid food (Hodgson, 1971c, d).

Another possibility is that calves, though receiving more solid food before weaning, are better adapted to it and so can increase the intake of solid food after weaning at a more rapid rate. In this

regard Hodgson (1971a) demonstrated that whereas after weaning the intake by calves of dried grass fed in the loose long form was dependent to a significant extent on the calves pre-weaning experience of it, this was not the case when the same dried grass was fed in the ground pelleted form.

If this general relationship between the intake of solid food before and after weaning is significant then it has important practical significance. In order to obtain a high intake of solid food after weaning, one has to forego performance pre-weaning because of the necessity of restricting milk to encourage the intake of solid food. The appropriate balance between these two factors is still far from determined. This is illustrated by the work of Aitken Present, Whitelaw, MacDearmid and Charleston (1963) and Owen et al., (1969) who showed that any advantage gained in liveweight pre-weaning with higher milk fed groups was lost in the subsequent post-weaning period, a result which was contradicted by Hodgson (1971c), Brookes and Davey (1975) and Morgan and Owen (1972, 1973) who showed that the advantage gained in the pre-weaning period with the higher levels of milk fed persisted despite a lower level of intake of solid food initially post-weaning.

Dietary Factors of Solid Food

To exploit a calf rearing system which uses a low level of milk feeding as does that developed by Preston (1957) and Khouri (1969) it is necessary to use a solid food which promotes a rapid increase in intake under the given milk feeding regime. As the young ruminant has a smaller rumen capacity and/or limitiations in its eating behaviour, the diet must be of high energy density. According to Fitzgerald and Kay (1974) no difference in intake or feed

utilization was found when an all concentrate diet was offered in the dry form or as 30%, 20% or 15% DM. In this study calves had continuous access to wet feed and consequently the conditioning effect associated with feeding of limited quantities of liquid feed in stimulating closure of the oesophageal groove was absent (Ørskov et al., 1970). Owen et al. (1969b) and Kay et al. (1972) demonstrated that lambs and calves were better able to compensate for energy dilution of the diet by coarse roughage (oat husks and chopped straw respectively) when the diet was pelleted. The advantages of pellets as opposed to meal is less apparent at low levels of roughage inclusion. Lassiter (1955) found that calves having free access to both pellets and meal, selected pellets in preference to meal, but when each was singularly and separately fed there was no significant difference in intake. This latter result was supported by Hardy (1972).

Recent work by Warner, John, Porter and Slack (1974) investigated bloating in young ruminant calves fed concentrates. Physiologically bloat has been a problem with low fibre concentrates (Preston et al., 1963) and Preston suggested fibre should be present to promote normal physiological activity. From the work of Warner et al. (1974) it would appear physical form of the fibre is more effective than fibre level as such. As they only dealt with mash and ground pelleted concentrate, comparison with other workers who used long hay and pelleted concentrate is impossible. It is interesting to note that Welsh and Smith (1970, 1971) have found that rumination time is affected both by fibre level and particle size. The work of Warner et al., (1974) supports these findings, the large particles eliciting an earlier and more consistent pattern of rumination. Warner et al.,

(1974) found the feed intake of the larger fibre particle mash was greater than the pelleted finely ground concentrate, the average daily gain being significantly greater even though conversion efficiency was lower for the mash. Kay (1969) cited experiments at the Rowett Institute which clearly showed that when care was taken during the processing (pelleting) of the diet to retain the husks on the cereal grains, calves did not suffer from bloat and they converted their food into body mass more efficiently than did calves offered the same diet in the loose form. Whole pelleted cereals were also found to be superior to ground pelleted cereals as food for early weaned calves.

Another major limitation of young ruminants would appear to be their immature buffering system. This can be overcome by adding buffers to their food (Preston, 1961; Kang and Liebholz, 1973), but for the long term benefit of the young ruminant some roughage is needed as Wilson (1963) concluded that the parotids grew and matured in response to mechanical stimuli provided by food.

It was mentioned earlier that because of the postulated prominence of oropharyngeal factors in controlling the intake of solid food in young ruminants shortly after weaning palatability of the solid food is important. The fact that calves are very selective grazers (Hodgson, 1968) may indicate palatability has an influence on intake. However palatability is difficult to define accurately and exactly, since it is a concept rather than a scientific term (Greenhalgh and Reid, 1971) and there is confusion as to whether it is important in influencing intake in adult ruminants. Balch and

Campling (1962) claim that it is unimportant in influencing the level of intake of a diet fed singly (a contention recently challenged by Baile and Mayer, 1967; Greenhalgh and Reid, 1971), but did consider it important in the initiation of eating.

Because of the problem in defining palatability it is difficult to know what factors are important in causing a palatability response. I propose to deal with the problem under three headings: Taste, Texture and Hardness.

Taste. In this respect a number of workers (Preston, 1956; Atai and Harshbarger, 1965; Gardiner, 1967) have demonstrated positive responses in DM intake when sweetening agents were included in the diets, indicating perhaps a palatability response.

Texture. Texture is another possible palatability factor, and Ray and Drake (1959) claimed that on intake evidence coarse textured concentrates are more palatable than fine textured ones. However texture in this context is probably confounded with the promotion of favourable rumen development caused by the coarse textured diet. Palatability does not appear to be important in influencing the choice of cereals for a concentrate ration, as Kay (1969) cited unpublished work of Kay and MacLeod showing that either wheat, barley or maize could be used interchangeably in the ration without affecting intake or production. This supports a conclusion of Caffrey and McAleese (1965) that the differences in palatability between cereals for calves are usually confounded by the preparation of the cereals.

Hardness. It has been suggested (Warner and Loosli, 1957; Bartley, 1973) that hard pellets (crushing over 13.0kg in a Stokes hardness tester) were less acceptable than soft pellets. Warner

et al., (1974) feeding a low fibre pellet (8.3kg Stokes hardness tester) and a high fibre pellet (12.0kg Stokes hardness tester) ad lib. to young ruminants found no difference in measured levels of intake. It should be pointed out here that both pellets types were not offered ad lib. at the same time to each group of animals.

In conclusion it would appear that the type of food most suitable for weaning calves is one which is "palatable" had a high energy density and promotes and overcomes the immaturity of the buffering capacity in the developing rumen.

III. PROTEIN AND ENERGY REQUIREMENTS

Nutrient requirement of animals are assessed to facilitate the formulation of their rations but to do this effectively it is essential to know:

(a) The total needs of the animal tissues for each nutrient;

(b) The capacity of the diet to provide the tissues with these nutrients.

The needs of the tissues for nutrients in similar animals in a particular physiological state should theoretically be fairly constant. However the availability of dietary nutrients to the tissues is highly variable and depends on many factors including the physical and chemical properties of the feed stuff, the methods used in their formulation and their apparent digestion.

Feed energy in most feeding systems (A.R.C., 1965; N.R.C., 1970) is partitioned into allowances for maintenance and production respectively. This division of energy metabolism does not imply exclusive separation in the life processes of the animal, rather one metabolism which at different parts of the body performs different jobs, i.e. maintenance and various kinds of production.

An animal deprived of food continues to require energy for those functions of the body immediately necessary for life - for mechanical work of essential muscular activity, for chemical work such as movement of dissolved substances against concentration gradients, and for the synthesis of expended body constituents such as enzymes and hormones. The maintenance level for an animal is the amount of energy required to keep the animal in zero energy retention and this value can depend on the amount of activity and the environment (Osuji, 1974). Production occurs as a result of the utilization of that portion of energy intake not required for maintenance.

The Balance of Energy Within an Animal

$$ER = MEI - HP \quad \text{or} \quad MEI = ER + HP$$

ER = energy retained

MEI = metabolizable energy eaten

HP = heat produced.

Measurements of energy metabolism

1. Calorimetry balance methods - direct and indirect.
2. Slaughter methods.
3. Inferences from measurement of liveweight gain.

Balance Methods

Energy balance is estimated by the difference between the heat of combustion of the food and the sums of combustion of excreta, including gases and the heat production of the animal measured over a time interval. Advantages of balance methods are:

1. no restriction - repetition of trial possible.

2. theoretically small energy retentions can be measured over short periods of time. The disadvantages will be dealt with under a general heading as well as those peculiar to each technique.

General Errors common to Balance Experiments

The balance method estimation of energy retention depends on random errors attached to five terms. These are mainly of a statistical nature arising largely from sampling difficulties and are of two types (Blaxter, 1967; Graham, Blaxter and Armstrong, 1958).

1. Analytical and instrumental errors.

2. Day to day variation in production of faeces, urine, methane, heat production and measurement of intake - sequential errors. Further details of these errors are given by Blaxter (1967). Itoh (1974) found the more steps involved in energy metabolism measurements the greater are the chances of a significantly large error creeping into measurements.

Direct Calorimetry. Measures total heat lost from the animal by measuring both sensible and evaporative heat loss, e.g. the "Gradient layer" techniques as described by McLean (1971) and Pullar (1958). Additional disadvantages of direct calorimetry include:

1. Basic assumptions giving rise to systematic errors. Errors due to heat losses in faeces and urine removed from the chamber, variations in evaporative heat loss determined by water vapour produced, differences in body temperature or stall temperature at the beginning and end of the trial (Blaxter, 1967). A more thorough discussion of errors is given by Graham, Blaxter and Armstrong (1958).

Indirect Calorimetry. As substances oxidized within the body fall into three main categories, carbohydrate, fat and proteins, the thermal equivalents of oxygen, or the amount of heat produced per litre of oxygen has been estimated for each of these three substrates. In order to apply thermal equivalents it is important to know how much oxygen is used by each substrate and this is calculated from the respiratory quotient, the concentration of carbon dioxide produced to oxygen consumed at normal temperature and pressure for each of the substrates. Most heat productions are now estimated from respiratory exchange and nitrogen excretion following the work of Weir (1949) and Brouwer (1965). Indirect calorimetry consists of open and closed circuit techniques. The open circuit system depends on the precise measurement of the changes in O_2 and CO_2 concentration of the air entering and leaving the calorimeter as well as the flow rate through the chamber. The closed circuit system differs from the one just described in that the same air is continuously circulated through the apparatus which is hermetically sealed. Moisture and CO_2 produced by the animal are rapidly removed by chemical absorbents; this causes a decrease in pressure within the system allowing oxygen to flow into the chamber from a weighed cylinder, and spirometer until pressue in the system is restored to equilibrium (Farrell, 1974).

Open circuit calorimetry has the advantage that chamber leaks are usually relatively unimportant as long as air entering the system is of uniform and constant composition. Temperature in the respiration chamber may be allowed to fluctuate during the measurement period and observations can be made successfully over short periods of time. A full discussion of the errors in respiration calorimetry is given by

Graham et al. (1958). Wainman and Blaxter (1958) and Flatt et al. (1958) give good discussions of closed and open circuit indirect calorimetry respectively. Comparisons made between heat production measurements on the same animals in open circuit and closed circuit calorimeters has shown good agreement (Winchester, 1940). Agreement between direct and indirect calorimetric techniques would appear to be very good (Webster, 1976). Balance methods because of the errors involved, tend to underestimate excreta thereby over estimating ME intake and energy retention. Further discussion of the errors involved in calorimetry can be found in the work of Blaxter (1967), Itoh (1973) and Howell et al. (1976).

Comparative Slaughter. Measures energy retention by the difference in heat of combustion between similar animals slaughtered at the beginning and the completion of a trial. Because no two animals are precisely similar large numbers are required if the error attached to energy retention is to be kept small. The method provides a direct measure of energy content limited only by analytical accuracy. While no elaborate apparatus is required, it is an expensive laborious and wasteful technique. The technique would be less costly if body composition and hence energy content could be measured non destructively in living or undissected carcasses. The use of tritiated water and dilution techniques (Searle, 1970) concentration of K in lean body mass (Kirton, 1963) and specific gravity studies (Garret and Hinman, 1969) have all been moves in this direction. Measurement of metabolizable energy intake is usually made at the beginning of the trial assuming methane production to be 8% of digestible energy intake (A.R.C., 1965) and is assumed constant throughout the trial. The

work of Blaxter et al. (1966) and Graham and Searle (1972a) appears to agree with this assumption.

Inferences from measurement of Liveweight Gain

These trials are usually of the balance type, in that they measure the amount of feed to give a certain gain and from this calculate feed to give no gain. Another method reported by McDonald et al. (1973) involves the analysis of energy intake (I) liveweight (W) and liveweight gain (G) by solving

$$I = aW^{0.75} + bG$$

where 'a' and 'b' are estimates of the quantity of food energy used for maintenance and each unit of liveweight gain respectively. Errors in this method when used to predict energy retention stem mainly from liveweight gain not being a very good measure of energy balance (Ørskov et al. 1976; Parker and Hutton, 1976; Rattray and Joyce, 1976). Along with comparative slaughter it has the advantage that animals are competing in their normal environment. Workers who have used and commented on this technique with calves include Brookes and Davey pers. comm.; Brisson et al. 1957; Bryant et al. 1967; and Roy et al. 1958.

Maintenance

Methods of measuring maintenance (Van Es, 1972) are:

1. From regression methods,
2. From measurements above below, and at maintenance,
3. From fasting heat production.

1. Estimates of maintenance requirements by means of regression methods

This method consists of extrapolating to zero intake the regression relationship between energy intake and retention.

$ER = K_g(MEI) - b$ or $ER = K_g(MEI) - ME_m)$

b = an estimate of true NE_m (net energy maintenance)

MEI = ME intake

Kg = efficiency of utilization of ME over and above that required for maintenance.

ER = energy retained or lost

This is the technique employed by Holmes and Davey (1976), Van Es (1972), Webster et al. (1974), Webster et al. (1976) and Vermorel et al. (1974). Using comparative slaughter to estimate HP (heat production)and extrapolating the regression of ME intake on heat production to zero intake, maintenance,is estimated as the point where ME intake equals heat production (Lofgreen and Garrett, 1968; NRC, 1970). This method is similar to the above in that it involves the extrapolation of a regression line. Workers who have used this method include Lofgreen and Garret (1968), Johnson (1972), Garret (1974) with cattle, Rattray and Joyce (1976), Ørskov et al. (1976) and Howell et al. (1976) with sheep.

Possible sources of error in extrapolating the regression of intake on energy retention are:

1. The energy content of weight gain changes with age and weight (Blaxter et al., 1966; Searle et al., 1972; Graham and Searle, 1972a; Orskov et al., 1976). Hedde and Knox (1970) claim the efficiency of ME used for maintenance and growth indicated a greater energy cost for the maintenance of lean than for the maintenance of fat with young calves, while later work of Graham and

Searle, 1972 (with sheep) found no differences. As the body weight and its composition is changing and as $ME_m = aW^p$ (where ME_m = maintenance requirement of ME, 'a' is a constant, W liveweight and 'p' an exponent of liveweight), is the exponent 'p' a constant $\frac{3}{4}$ as proposed by Kleiber (1965) or does it vary during the rapid growth phase (Blaxter, 1972; Graham, 1970; Mount, 1968)? The slope of the curve $ME_m = aW^p$ is steeper and changes more at low than at high levels of W so it is more important to know the correct value of p for the young than the older, heavier animals (Van Es, 1972). This change in the exponentof liveweight may affect the correction of metabolic results for weight changes in experiments where there are differences in liveweight between treatments. Blaxter et al. (1966)discussed at some length systematic errors in the calculation of efficiency of utilization of metabolizable energy (and hence the intercept, ME_m) induced by a scaling based on body weight determinations.

2. The relationship between energy retention and production may not be linear especially at higher intake levels relative to maintenance, but present results (Blaxter, 1962; Graham, 1970; Graham and Searle, 1972b) would suggest that it is.

3. There is some disagreement about the energetic cost of the production of protein compared with that of fat, (Buttery and Boorman, 1976; Kielanowski, 1976; Rattray and Joyce, 1976 and Ørskov and McDonald, 1970). If protein synthesis is less efficient than fat synthesis (reviewed Buttery and Boorman, 1976) as the proportion of protein produced to fat changed during growth

(Lofgreen and Garrett, 1968) this would influence the regression.

4. The range of intakes will affect the accuracy of the extrapolation - especially if intake was very similar and at a high level in all experimental animals. Ideally as wide a range of ME intakes as possible ranging from near maintenance intakes to ad. lib. levels would involve the smallest error (Van Es, 1972). It should also be noted that metabolizability of diets above 16% crude fibre decreases with increasing level of intake.

5. The efficiency of utilization of energy for maintenance and especially production depends on the dietary source of energy (Blaxter, 1974; A.R.C., 1965; Blaxter, 1967).

Whether the efficiency of utilization of ME for gain decreases (Armstrong and Blaxter, 1957; Armstrong et al., 1958; Blaxter and Wainman, 1964) or remains unaltered (Elliot et al., 1965; Ørskov and Allen, 1966a, b, c; Bull et al., 1970) as the molar proportions of acetate from a diet increase has been a point of conjecture for many years. Reviewing past experimental techniques and their associated errors as well as presenting their own results from calorimetric and slaughter trials, Howell et al. (1976) conclude that the efficient utilization of acetate may depend upon a supply of glucose or a glucose precursor. This premise may explain some of the measured response differences cited in the literature.

6. Regression computations theoretically require that the independent (ME and ER are related) variable (s) do not contain measurement errors. It is probable in calorimetric energy balance experiments that ME intake will be overestimated (Blaxter, 1967) and as a consequence energy retention is also overestimated increasing the regression coefficient (Kg). In the comparative

slaughter approach animals, because they are not in confined heat controlled chambers as in calorimetry, will tend to have higher maintenance heat productions because of temperature fluctuation and activity (Howell, et al., 1976). This will result in smaller regression coefficients (K_g) than calculated from calorimetry. Balance experiments and slaughter techniques contain errors which tend to accumulate which may also explain differences in K_g of up to 20% (Howell et al., 1976).

7. Growing animals usually show decreased muscular activity with age (Van Es, 1972).

For accurate use of this method, a wide variation of intakes are required, preferably over a range of weights in which maintenance cost per unit metabolic body weight are fairly constant.

From Measurements above, below and at maintenance

This method consists of performing two or more energy balance trials with a number of animals feeding a ration at levels close to above and below maintenance respectively. The techniques of comparative slaughter and calorimetry have been used here (Blaxter et al., 1966; Van Es, 1972) as well as liveweight gain trials. If as Blaxter et al. (1966) and Blaxter et al. (1974) assume gut fill does not increase maintenance requirement, then organization of trials in such a way that changes in tissue gain are negligible could be used without objection (Van Es, 1972). A good review of the techniques used and their shortcomings is given by Van Es (1972). Problems in using liveweight gain techniques include:

1. Small changes in body weight are difficult to measure in ruminants because of gut fill and irregular patterns of excretion of faeces and urine (Stobo and Roy, 1964; Johnson, 1972).

2. Energy content of the LWG (liveweight gain) may change (Ørskov et al., 1976; Blaxter et al., 1966; A.R.C., 1965; Lofgreen and Garnet, 1968; Graham and Searle, 1972a, 1972b).

3. Feeding rations for short periods of time may involve errors in estimation of digested food.

Because the energy concentration of liveweight gain increases with age and weight (Blaxter et al., 1966; Graham and Searle, 1972a, 1972b; A.R.C., 1965; Lofgreen and Garret, 1968) and these increases are hard to monitor, techniques involving calorimetry or comparative slaughter should be used.

From Fasting Heat Production

Fasting heat production is a measure of basal energy metabolism, in a thermoneutral environment, in a post absorptive condition, uncomplicated by heat increments incident to feed utilization and high or low environmental temperatures. Because starved animals tend to be active, lying down and standing, which requires differing amounts of energy (Blaxter, 1962; A.R.C., 1965; Osuji, 1974) and the concept of Basal energy metabolism involves no activity, the term (F.H.P.) fasting heat production is used for animals, except where the measurements are made over a short period of inactivity, e.g. sleep. It should be remembered that the heat produced by a fasted animal results from the true net energy of maintenance plus the heat increment due to the energy cost of mobilizing the substrate for

maintenance and the energetic inefficiency of ATP generation for maintenance from the substrate in question (McDonald et al. 1973). The heat production of fasting animals is measured to provide a baseline from which the effects of ingested food on energy metabolism can be evaluated, and to determine the relation between liveweight and heat production. The heat increments of foods determined below maintenance represent not the true inefficiency of energy conversion, but inefficiency relative to that of the utilization of body reserves, so (Km) efficiency of utilization of food energy below maintenance, is different in concept to K_g which is a true net efficiency. Heat increment is a measure of the energetic costs of the process of digestion and the energetic inefficiency of the reactions by which absorbed nutrients are metabolized.

Measurements of FHP are made by both direct and indirect calorimetry. These are completely different to FHP's quoted from slaughter experiments that are obtained by extrapolation of the regression relating ME intake to heat production from above maintenance levels of intake to zero ME intake (Lofgreen and Garret, 1968; Garret, 1970) and are probably measures of the true net energy of maintenance.

Techniques of measuring heat production vary in their length of fast, extent of activity of animals being recorded, and length of measurements. Some workers (Deighton, 1929 and 1937 and Brody and Kibler, 1944) only measured the heat production of their pigs over short periods of sleep or inactivity compared with 24 hour measurements such as Holmes and Davey (1976) with calves, which almost certainly included activity. Roy et al. (1957) striving to obtain basal metabolic rates go to great lengths to describe their physical

restraint techniques. Calves in such situations must be under considerable stress which in itself is known to increase heat production (Van Es, 1972). The post absorptive state in animals is reached after different periods of time. RQ's (respiratory quotients) close to 0.7 or a complete fall off in methane production being the best indicators (Blaxter et al., 1962). Waiting for RQ's to reach 0.70 can put the animal under considerable stress from other sources and several workers suggest that rather than stabilizing, heat production progressively declines (Blaxter and Wood, 1951; Mitchell, 1962). Holmes and Brierem (1974) give some indication of the size of the inaccuracies likely to creep into measurements of FHP over extensive fasts, with pigs. Van Es (1972) summarizes the effects likely to increase FHP.

1. Measurements below critical temperature (Holmes and McLean, 1975)
2. Nervousness (Van Es, 1969; Blaxter et al., 1966).
3. Determinations before the post absorptive state is reached (Holmes and Davey, 1976).
4. Activity (Brody and Kleiber, 1944).

Analysis of a large series of fasting metabolism measurements similar to that undertaken by Graham et al. (1974) in sheep with the derivation of a prediction equation for FHP encompassing metabolic weight, age, prior weight gain and pre-fasting intake of energy would appear the best method to obtain some consistency in measured FHP's. When Holmes and Davey (1976) used the prediction equation (5) for lambs of Graham et al. (1974) and substituted their mean values for liveweight gain and digestible energy intake, predicted values of FHP were very close to those measured with calves.

Interpretation of FHP can be difficult.

Holmes and Davey (1976) reviewing FHP's in young calves found obvious discrepancies where FHP's were greater than the accepted maintenance figures thus requiring Km values of greater than 100%. Errors inherent in direct and indirect calorimetric measurement of HP will also apply here (Blaxter, 1967).

The use of FHP for calculating maintenance has been criticised recently by Webster et al. (1974) on the grounds that FHP does not entirely reflect some property of the animal. It is in part dependent on:

i. previous dietary history (Martson, 1948; Graham et al., 1974; Mitchell, 1962).

ii. whether stabilization or a progressive decline in HP sets in (Blaxter and Wood, 1951; Mitchell, 1962).

Metabolic adjustments under fasting will depend on the relative amounts of fat and protein available to sustain metabolism and the rates at which protein and fat were anabolized prior to starvation, however neither factor has any direct bearing on metabolism during uninterrupted growth.

Factors Affecting Maintenance

1. Level of activity (Osuji, 1974; Van Es, 1972).

2. The influence of body weight. Brody and Proctor (1932) and Kleiber (1932) independently came to the conclusion that basal metabolic rate (BMR) per Kg^x of body weight, where 'x' was approximately $\frac{3}{4}$ was relatively constant across many species of homeotherms and they promulgated the useful concept of metabolic body size generally accepted (Kleiber, 1965). Although this consistency in adults is generally accepted, it has long been known that BMR per $kg^{\frac{3}{4}}$ can be much higher in young animals (Brody, 1945;

A.R.C., 1965; Cooke, 1968; Webster et al., 1974) and there is reason to believe that this is influenced by growth rate in the young or by the rate of tissue regeneration in adults (Brody, 1945; Graham et al., 1974). Van Es (1972) cites Schiemann (1958) who found 1.0 was more appropriate than 0.75 in fattening steers. 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 (Van Es, 1972).

3. Composition of the ration (Blaxter, 1974; Lofgreen and Garret, 1968). As mentioned earlier, Km, efficiency of utilization of energy use for maintenance, is a measure of the efficiency of utilization of the ingested food relative to those of body reserves in meeting the energy costs of maintenance. When an animal is given food HP will increase above BMR because:

i). The process of digestion, mastication and propulsion of food in the alimentary tract requires energy (Blaxter, 1962; Baldwin, 1968; Osuji, 1974). The cost of this energy varies with the nature of the diet (Graham et al. 1974).

ii). Heat arising from the activity of micro organisms - heat of fermentation, usually about 5-10% of gross energy of food (McDonald, et al., 1973).

iii). The energetic inefficiency by which absorbed nutrients are metabolized to provide ATP for maintenance (Blaxter, 1962; Armstrong and Blaxter, 1957). Numerous workers have shown that for maintenance the efficiency of utilization of ME from different dietary sources varies very little whether the estimates were calculated from calorimetric or comparative slaughter data (Armstrong and Blaxter, 1957; Armstrong et al., 1957; Brouwer et al., 1961; Van Es, 1961, Blaxter, 1961, 1967; Armstrong, 1964; Blaxter and Wainman, 1964).

iv). The influence of temperature (Blaxter, 1962; Holmes and McLean, 1975; Webster et al., 1970; Gonzalez-Jiminez and Blaxter 1962; Blaxter and Wainman, 1964).

v). Influence of weight and age (Blaxter et al., 1966; Graham and Searle, 1971; Ørskov et al., 1976).

vi). Between animal variability. This may be as high as 5-10% Van Es (1972). There also appears to be between breed variations (Webster et al., 1976; Vercoe and Frisch, 1974).

Energy Retention - Production

Energy retained is measured either indirectly by calorimetry both open circuit and direct, or directly by comparitive slaughter. Metabolizable energy is usually regressed against energy retention as shown below. ER = k_g MEI - b. ER and MEI are not independent in balance type experiments but are independent in slaughter work.

ER = Energy retained

k_g = Efficiency of utilization of ME for growth (fat and protein)

MEI = Metabolizable energy intake

b = An estimation of NE_m.

Reasons for possible discrepancies between kg values measured by calorimetry and slaughter techniques:

1. Animals confined to calorimeters perform in thermoneutral environments compared with the less confined slaughter animals subject to the day to day environmental fluctuations.

2. Calorimetric balances and slaughter techniques involve errors as previously mentioned which cover the scope of the difference in kg measured by the two techniques (Howell et al., 1976). E.g. calorimetric techniques tend to underestimate faecal losses consequently over-estimating ME intake and energy retention (Blaxter, 1967).

3. Other variables as previously mentioned which affect maintenance. A comprehensive coverage of factors affecting the slope and intercept of this regression equation was given in the maintenance section.

Efficiency depends largely on the efficiency of metabolic pathways involved in fat and protein synthesis from the absorbed nutrients (Blaxter, 1962). The processes of anabolism are more complicated and energy demanding than those of catabolism (McDonald et al., 1973), because materials must be in the right proportions at the right time in the right place. This complexity makes theoretical calculations of efficiency difficult, if indeed not meaningless (Buttery and Boorman, 1976).

Factors Affecting Kg

1. Storage of energy as protein or fat

Protein percentage decreases and fat percentage increases as the animal approaches mature body weight (Blaxter, 1966; Lofgreen and Garret, 1968; A.R.C., 1965; Graham and Searle, 1972). Blaxter et al., (1966) and Baldwin (1968) claim the theoretical efficiency of protein synthesis is slightly greater than that of fattening, but when the energy costs of deposition are calculated according to the technique first outlined by Kielanowski (1965) the efficiency of protein deposition is less than that of fat deposition and far more variable (Buttery and Borman, 1976; Kielanowski, 1976) also see Table 2.2 The discrepancy between the theoretical and measured value of efficiency of protein deposition may be accounted for partially by the process of protein turnover (Buttery et al., 1975; Nolan, Norton and Leng, 1973),

the excretion of excess nitrogen (Buttery and Boorman, 1976), the unlikelihood of achieving a completely balanced amino acid supply, and the transport of amino acids. Kielanowski (1976) found the measured cost of fat deposition agreed very closely to those deduced from biochemical considerations (Armstrong, 1969). Because nutritional balance trials tend to overestimate nitrogen retention and consequently underestimate the cost of protein deposition, Kielanowski (1976) only includes within his quoted material, nitrogen retentions calculated by comparative slaughter. From the tables of Kielanowski (1976) it appears that the energy cost of protein deposition is lower in younger rather than older animals. This may be due to:

1. The proportion of amino nitrogen in total nitrogen in the body increasing with age, e.g. work with rats cited by Kielanowski, 1976.

2. The fraction of free amino acids in the body decreasing with advancing age due to the relative decrease in body fluids. This means the older animal retains more true protein than its younger counterpart for the same amount of nitrogen retained.

Various alterations have been made to the original model as proposed by Kielanowski (1965):

$$MEI = a\,M^{n} + b\,P + CF + i$$

In energy balance techniques $P + F = ER$ and $ER = ME - HP$ so the so called independent variables are related.

MEI = Metabolizable energy intake, M^{n} is a maintenance term expressed as an exponent of body weight, P = protein deposition in ('g' or KJ), F = fat deposited (g or KJ), a, b, c and i are constants, b representing the cost of depositing a unit of protein (KJ/g or KJ/KJ), c, the similar coefficient for fat and 'i' representing an intercept term. The necessity for the intercept term (McCracken,

1973), the meaning of the maintenance term and the interdependence of the coefficients (Ørskov and McDonald, 1970 and Rattray and Joyce, 1976) have been commented on. The energetic efficiencies of utilization of ME for fat and protein deposition (KJ of fat or protein/KJ ME required X 100) measured by Rattray and Joyce (1976) in sheep fed a variety of diets range from 76.7 - 82.3 and 10.4 - 20.5% respectively. It would appear from the literature even with the possible errors which might be introduced by high correlations between supposedly uncorrelated variables, that protein deposition is much less efficient than that of fat. Most estimates of efficiency of utilization for total energy gain in ruminants determined by comparative slaughter lie in the range 30-50% (Lofgreen and Garret, 1968) which would appear to correspond to compositional changes in liveweight gain. Blaxter et al.(1966) using calorimetric techniques, Garret (1970) using slaughter techniques (cattle), and Graham and Searle (1972) (sheep), using tritiated water to estimate energy and protein retention found the efficiency of energy and protein utilization in the ruminant animal varied little with stage of growth. Van Es (1967) included percent energy retained as protein as an independent variable in his regression equations $ER/kg^{0.75} = aME/W^{0.75} + bP + d$ (bP = % protein, d = intercept) and obtained no improvement. Along with Blaxter et al.(1966) he concluded that within the usual range of proportions of protein and fat energy to total retained energy during growth, there is little to be gained from establishing separate efficiencies for protein and fat deposition nor much change in k_g due to changes in composition of tissues deposited.

TABLE 2.2: Estimates of the ME cost and efficiency of fat and protein deposition in different animals

Animals	Method	Fat Deposition KJ ME/g	Efficiency (%)	Protein Deposition KJ ME/g	Efficiency (%)	Source
Sheep						
Milk fed	Comparative slaughter	63	61	30	78	Kielanowski (1965)
Milk fed	Calorimetry	30	84	58	65	Walker & Norton (1970)
Early weaned concentrate	Comparative slaughter	48	80	68	34	Ørskov & McDonald (1970)
(Ruminant) over 6 months	"	43	89	191	12	Rattray et al. (1974)
(Ruminant) over 6 months	"	49	79	114-225	10-20	Rattray & Joyce (1976)
Pigs						
Young milk fed	"	49	78	31	75	Kielanowski (1965)
Castrates (30-90 kg)	"			67	34	Kotarbinska (1969)
Castrates (25-110)[1]	Calorimetry			46	51	Oslage et al. (1970)
Growing (10-90)	Comparative slaughter	54	71	67	35	Kielanowski & Kotarbinska (1970)
Growing (10-90)	Calorimetry	52	74	54	43	Thorbek (1970)
Growing (10-90)	Comparative slaughter	68	57	49	48	Sharma & Young (1970)
Rats						
	Calorimetry	59	65	53	44	Pullar & Webster (1974)
	Calorimetry	51	76	27	86	McCracken (1973)
*	Calorimetry	56	70	48	48	Schieman et al. (1969)
Calves						
Young milk fed	Comparative slaughter	37	100	65	36	Donnelly (1975)
Young milk fed[1]	Calorimetry	50	79	44	54	Holmes & Davey (1976)
32-145 kg[1]	Comparative slaughter			58	40	Osinska (1974)

* Energy content of deposited protein assumed to be 23.3Kj/g
Energy content of deposited fat assumed to be 38.9 Kj/g

2. Physiological State

Differences in efficiency exist between non ruminants and ruminants because of the different end products of digestion and the heat of fermentation involved in ruminant digestion (McDonald et al., 1973; Blaxter, 1962; Van Es, 1967). Graham and Searle (1972b) working with sheep from birth to two years of age, found efficiency of energy and protein utilization declined at weaning from milk to solids but otherwise did not vary much with stage of growth. A similar trend is apparent in cattle, by comparing the kg values of Van Es(1969), Johnson (1972) and Holmes and Davey (1976) working with pre-ruminant calves with those of Blaxter et al. (1966) working with older growing ruminant cattle.

3. Sex

In comparative slaughter trials with cattle Garret (1970) found no significant difference between steers and heifers in the efficiency of utilisation of ME for growth, even though gains made by heifers contained higher levels of fat and higher concentrations of energy/kg of gain.

4. Diet type

Factors which affect the ME values of food; crude fibre level (Blaxter, 1974; Webster et al., 1974), ration composition (Blaxter 1962; Hovell et al., 1976), preparation of food, physical form, and level of feeding (McDonald et al., 1973) may also affect the form in which ME is absorbed and hence possibly its efficiency of utilization for production. As mentioned previously, Hovell et al. (1976) suggests that the efficiency of utilization of acetate may be similar to the other VFA's if an adequate supply of

a glucose precursor is available. Another dietary factor is the level of protein in the diet. Efficiency of energy utilization for gain decreasesif animals are fed diets of high protein levels, e.g. (Donelly and Hutton, 1976and Van Es et al., 1969)with calves, Hartsook and Hershberger (1971) with rats and Walker and Norton (1971) with lambs.

5. No significant differences for any length of time were found for 'kg' in animals undergoing compensatory growth (Ørskov et al., 1976; Graham and Searle, 1975).

Energy Retention per unit of Gain

The energy composition of gain varies because of the differing levels of fat and protein constituting the gain. Factors affecting the composition are stage of growth (A.R.C., 1965; Lofgreen and Garrett, 1968; Graham and Searle, 1971; Searle, 1970), sex of the animal (Garret, 1970), diet type (Donnelly and Hutton, 1976; Ørskov et al., 1976), compensatory growth (Graham and Searle, 1975; Ørskov et al., 1976) and breed (Searle and Griffith, 1976).

Energy retained can be measured by calorimetry both direct and indirect and comparative slaughter. For reasons mentioned earlier accuracy of measurements obtained by comparative slaughter are preferred. These energy retentions are then used in a regression of liveweight gain on energy retention for animals at the same stage of growth.

Some misunderstanding may arise over definition of terms. Energetic efficiency is MJ's retained/MJ's consumed (MJ = megajoules) while feed conversion efficiency is body weight gain/MJ's consumed.

TABLE 2.3: Maintenance expressed in MJ of metabolizable energy per unit metabolic weight

Authority		Maintenance MJ/kg$^{0.75}$	Technique	Diet
Blaxter and Wood (1951)	(c)	0.58	FHP Calorimetry	Milk
Bryant et al. (1967)	(c)	0.53	Growth & balance (LWG)	Milk
Brisson et al. (1957)	(c)	0.50	Growth & balance (LWG)	Milk
Roy et al. (1958)	(c)	0.56	Growth & balance (LWG)	Milk
McGillard et al. (1969)	(c)	0.45	Growth & balance	Milk
Van Es et al. (1969)	(c)	0.45	Energy balance Calcrimetry	Milk*
Johnson (1972)	(c)	0.42	Comparative slaughter	Milk
Davey and Holmes (1975)	(c)	0.37 - 0.41	Energy balance Calorimetry	Milk
Vermorel et al. (1974)	(c)	0.40	Energy balance Calorimetry	Milk*
Neergaard L. (1974)	(c)	0.42	Open circuit calorimetry	Ruminant concentrate mixture
Neergaard L. (1974)	(c)	0.43	Open circuit calorimetry	Ruminant concentrate mixture
Neergaard L. (1974)	(c)	0.42		
NRC (50 kg)[a] (1971)	(c)	0.50	Comparative slaughter	Milk*
ARC (50 kg) (1965)	(c)	0.63	FHP Calorimetry	Milk
Blaxter et al. (1966)		0.55	Energy balance Calorimetry	Ruminant concentrate mixture
Webster et al. (1975)	(c)	0.62	Energy balance Calorimetry	Non ruminant milk replacer
Webster et al. (1976)	(c)	0.67	Energy balance Calorimetry	Non ruminant milk replacer
Lofgreen & Garret[a] (1968)		0.54	Slaughter	Heifers 100% roughage
Lofgreen & Garret[b] (1968)		0.56	Slaughter. Heifers	3 levels 100% roughage
Lofgreen & Garret[b] (1968)		0.43	Slaughter. Heifers	3 levels 2% roughage
Ferrel et al. (1975)		0.39	Comparative slaughter(mature cow,	nonproductive) Concentrate fed
Hedde & Knox (1976)[a]	(c)	0.57(8-16 weeks)	Energy balance	35% milk* 65% concentrate
Garret (1970)		0.48	Comparative slaughter	Heifers steer concentrate ration
Lofgreen & Garret (1968)[b]		0.46	Comparative slaughter	3 levels 25% roughage

a. Maintenance calculated from the regression line of MEI versus heat production forced through the 'Y' intercept of 0.32 MJ/kg$^{0.75}$.

b. Calculated from data of Lofgreen and Garret (1968) by use of the regression MEI on ER, maintenance being when ER = 0.

* Milk replacer.

c. Calves (40-260 kg).

This is why Lofgreen and Garret (1968) who use the latter term, appear to disagree with the general trend of work (Kielanowski, 1976) which finds fattening energetically more efficient than protein synthesis. The fattening process is characteristically more efficient than protein deposition, but a fattening animal requires more energy per unit of gain because of the high energy density of fat and because the fat free portion of the gain is approximately 70% water (Rattray and Joyce, 1976). It would appear therefore that gains relatively high in fat are more efficient energetically but less efficient as feed conversion, than gains of relatively low levels of fat as found in young growing animals (Blaxter et al., 1966).

Values for Maintenance in Cattle

Values from the literature for maintenance are shown in Table 2.3 It should be pointed out that the NRC (1971) system of energy requirements follows that prepared by Lofgreen and Garret and all regressions of MEI versus HP are forced to intercept the 'Y' axis at .322 $MJ/kg^{0.75}$. This will undoubtedly alter the maintenance requirement when compared with those of other comparative slaughter experiments. In experiments where the actual measured data determines the HP intercept, the HP intercept should be comparable with energy balance determinations of maintenance.

Animals confined to respiration chambers would be expected to have a lower maintenance than less confined more active animals subject to variations in environmental temperature (Hovell et al., 1976). It would appear also that diet type is of greater importance than earlier stressed, as heifers between 230-500kg weight had maintenance values of .56 $MJ/kg^{0.75}$ and .43 $MJ/kg^{0.75}$ on 100% and 2%

roughage respectively fed at low, medium and ad lib. levels (Lofgreen and Garrett, 1968). Possible reasons for discrepancies in the earlier work with calves (Blaxter and Wood, 1951; Bryant et al., 1967; Brisson et al., 1957; Roy et al., 1958) may be due to:

1. The small number of calves used by earlier workers.
2. The health of the experimental animals.
3. The facilities available, length of fast, past diets, age and liveweight gain (Graham et al. 1974).
4. The use of live mass to assess response to treatments (Johnson, 1972).

A.R.C. (1965) based their energy requirements of young calves on the fasting heat productions measured by Blaxter and Wood (1951) on two calves and those of Ritzman and Colovos (1943) who found fasting heat production decreased as the animal matured. Later work (Holmes and Davey, 1976; Graham et al. 1974) suggests FHP may not be as high as first thought.

Considering the other values in the Table 2.3 those of Webster et al. (1975, 1976) are unexplainably high. Webster et al. 1976 go to great lengths to find possible reasons for their high values for maintenance compared with contemporary values and offer no worthwhile explanations.

Minor discrepancies between other values may be due to:

1. Differences in estimation of energy retention from calorimetric and slaughter techniques.
2. Diet types with differing K_g.
3. Ways in which maintenance was estimated.

These points were dealt with previously.

TABLE 2.4: Values from the literature for efficiency of utilization of ME for gain and energy retained per kg of gain

Authority	K_g	ER/kg LWG	Physiological State	Age or weight	Comments
Holmes and Davey (1976)*	.63 - .71	16.12	Pre ruminant	40 days	0.62/day
Johnson (1972)	.63	17.46	"	1-24 days	0.69/day
Van Es et al. (1969)*	.69	14.45	"	40-150 kg	Rapid growth
Armstrong (1969)*	.63	-	"	-	-
Vermorel et al. (1974)*	.69	-	"	40-160 kg	Rapid growth
Neergaard (1974)	0.52	-	Ruminant	115-260 kg	Concentrate & roughage diet
	0.51	-	"	"	"
	0.57	-	"	"	"
Walker & Norton (1970)* (milk fed lambs)	.68	8.79	"	5 kg	0.16/day
Blaxter et al. (1966)*	.50	-	Ruminant (steers)	80-300 kg	30 roughage
Webster et al. (1975)*	.70	-	Pre ruminant	80-180 kg	Rapid growth
Webster et al. (1976)*	.72	-	Pre ruminant	100-190 kg	Rapid growth
Blaxter & Wainman (1961)	.51	-	Ruminant (steers)	400-500 kg	
Lofgreer & Garrett (1968)	.25	-	Ruminant (heifers)	250-500 kg	100% diet roughage
Lofgreen & Garrett (1968)	.45	-	Ruminant (heifers)	250-500 kg	2% roughage
Garret (1970)	.47	-	Ruminant (heifers)	193-433 kg	15% roughage & concentrate
Hedde and Knox (1974)	.75	-	Transitional	2-4 months	
Ferrel et al. (1975)	.40	20.65	Non pregnant heifers		

* Either direct or indirect calorimetry. The remainder comparative slaughter.

Production

Trends in (K_g) values follow the same trends found in sheep by Graham and Searle (1972) with higher values preweaning levelling off post-weaning to a fairly constant value, independent of live-weight. The differences in K_g values with the different levels of roughage are very marked (Lofgreen and Garret, 1968). Apart from the errors involved in calorimetric determination of ER (Blaxter, 1967) it must be remembered comparative slaughter trials use digesta free body weight and body weight gains for their energy balance determinations, unlike calorimetry, where liveweight and liveweight gains independent of gut fill are not used. Blaxter et al. (1966) demonstrated mathematically that scaling of metabolic observations in which differing amounts of food are given to ruminants by a scaling parameter based on liveweight can lead to overestimation of efficiencies of feed utilization (Blaxter et al., 1966). Other possible causes of variation in results have been discussed earlier and include diet type, tissue being laid down, stage of growth, diet preparation and intake.

Protein Requirement of Young Calves

Most estimates of protein requirements in calves have been determined either as:

1. That level of protein intake above which no further increase in some measured criterion such as liveweight is achieved

E.g. The point at which nitrogen retention ceases to increase with increasing protein intake (Donnelly and Hutton, 1976; Stobo and Roy, 1973; with calves, Black 1970; Black et al. 1973; and Black and Griffiths, 1975 with sheep).

Donnelly (1975) presents an excellent review of the techniques and their associated errors used in estimating protein requirements.

These type of estimates are applicable only to the very limited conditions imposed by the particular experiments and could therefore vary widely between experiments. If however the total requirements of the tissue for amino acids is known (see review Lewis and Mitchell, 1976) it may be possible to accurately formulate diets by using estimates of the availability of amino acids from different feed stuffs.

Requirement of tissue for protein may be estimated from feeding trials by measuring response in N retention to changes in protein intake if:

(a) absorption of amino acids can be accurately assessed;

(b) efficiency of utilization of the absorbed amino acids is taken into account.

Efficient utilisation of absorbed amino acics depends on:

1. How closely the amount and pattern of absorbed amino acid meets the requirements of the animal's tissue.

2. The availability of energy in a biologically suitable form in relation to the amino acid absorption.

3. The availability of certain micro nutrients which are required either directly in the formation of peptide bonds or in other reactions involved in amino acid metabolism or ATP production.

To obtain a concise definition of the tissue requirements of animals for nitrogenous compounds it is essential to define:

(a) The total nitrogen requirement of the animals.

(b) The minimum about of this total N requirement which must be supplied from each of the essential amino acids, and how

(c) these requirements are influenced by the physiological state of the animal and the environmental conditions.

Black et al. (1973) proposed a method of measuring N requirements for lambs which may also be appropriate for calves which expresses these requirements in terms of reference protein (maximum nitrogen retention + total endogenous N loss X 6.25), as the precise requirements for essential amino acids of the growing animal in question are as yet undetermined. Crude protein (CP) may be estimated from reference protein by the following calculation:

$$\text{C.P req.} = \text{g Ref. protein} \times {}^{1/}\text{Efficiency of conversion of absorbed amino acids to protein} \times {}^{1/}\text{Efficiency of absorption of the amino acids of crude protein}$$

Requirements are usually expressed as grams of reference protein/MJ NE this being done on the assumption that:

1. N balance gives an accurate estimate of N retained (Black et al., 1973).
2. Endogenous losses can be calculated by extrapolation to zero N intake (Carr et al., 1975; Black and Griffith, 1975).
3. The obligatory N losses/$kg^{0.75}$ will be constant over the range of diets and liveweights in question.
4. The energy required for maintenance/$kg^{0.75}$ will be constant over the range of liveweights and diets in question Blaxter et al. 1966).
5. The efficiency of utilization of ME for maintenance and production will be constant over the range of diets and liveweight in question. Errors in the method are discussed in detail by Black, et al. (1973).

Possible Differences between non ruminants and ruminants

Factors which may be involved here are:

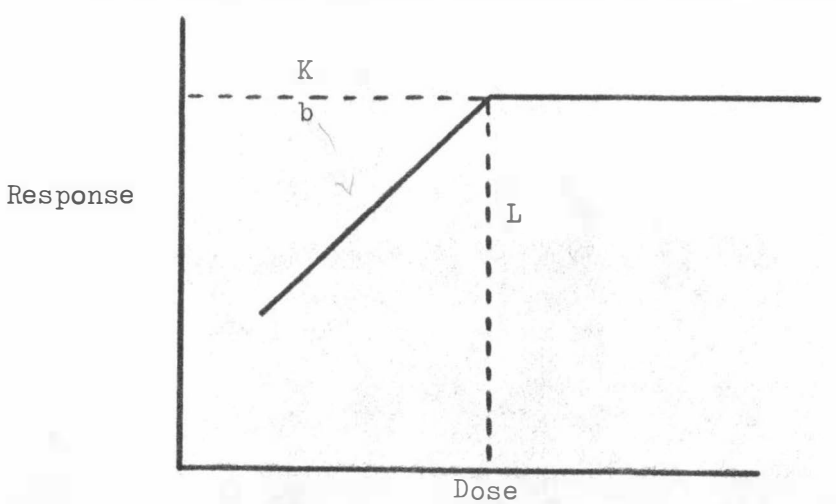
1. Effect of absorption of VFA's instead of carbohydrates and long chain fatty acids on the amino acid (AA) metabolism of animals.

2. Gluconeogenic reactions involving substantial amounts of AA's - so protein requirements/unit of ME may be higher than for non ruminants (Lewis and Mitchell, 1976).

3. Absorption of different end products of digestion may lead to alterations in secretion of hormones which influence amino acid metabolism.

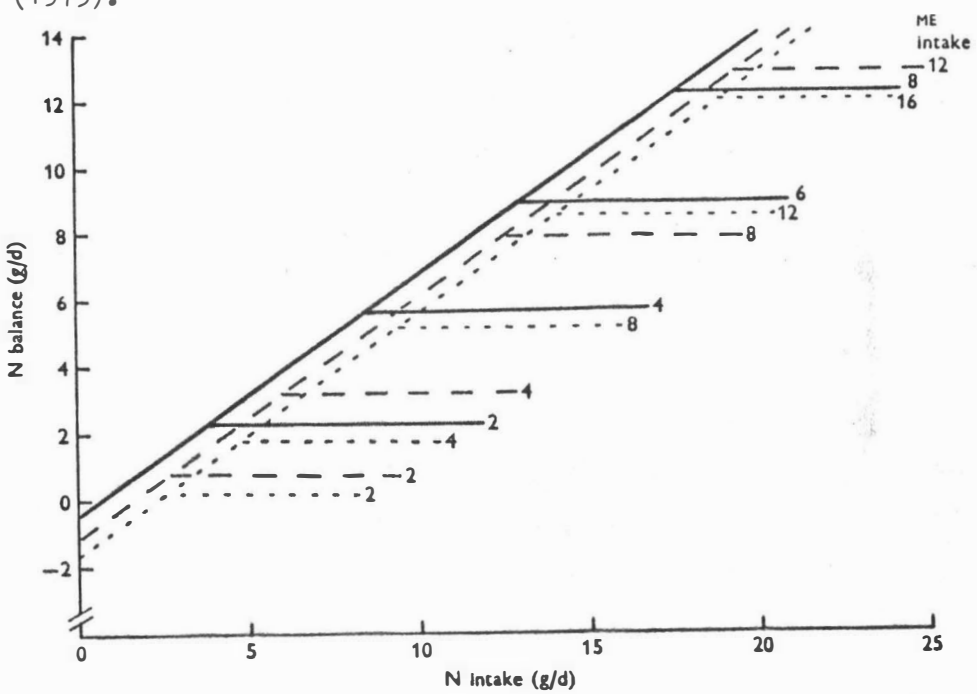
4. Allowing for the difference in gut fill between the ruminant and non ruminant calf (Johnson, 1972; Stobo and Roy, 1964).

Because maximum N balance of animals is dependent on energy intake it is important to specify energy intake as well as protein intake when defining protein requirements (Black et al., 1973; Carr et al., 1975; Preston, 1966; Balch, 1967, Ørskov, 1970). The technique used by Black and Griffith (1975) which is a further development of the technique first developed by Hegsted (1964) represents the overall relationship between N balance and protein intake as a step wise linear regression as shown below in Fig. 2.2



The relationship between dose and response (Hegsted, 1964) where 'b' is increase in gain with extra digestible N intake, K the maximum gain and L the minimum intake of digestible N for maximum gain.

b - represents rate of gain with each extra unit of N intake. K - represents the maximum gain and 'L' the minimum level of N to achieve this gain. Least squares analysis was used to fit the two linear functions. Other estimations of total N requirement may be criticised on the basis that they do not take into account the effects of both weight and metabolizable energy intake. Fig. 2.3 shows the fitted relationship developed by Black and Griffith (1975).



Fitted relationship between nitrogen balance and N intake for liquid-fed lambs differing in live weight (——, 5 kg; – – – –, 15 kg; ----, 25 kg) and metabolizable energy (ME) intake (MJ/d).

From Black and Griffiths (1975)

Total N requirement (g/d) = $aME - bW^{0.75} - cW^{0.75} \times ME + d(W^{0.75})^2$ where $W^{0.75}$ is body weight to the power 0.75 and ME is metabolizable energy intake, a, b, c, d being constants (Black and Griffith, 1975). Summarizing Black and Griffith's (1975) findings:

1. When N intake was insufficient, then nitrogen retention was independent of ME intake, similar to the findings of (Munro, 1964).

2. Under adequate protein absorption - nitrogen retention is influenced by liveweight (Preston, 1966; Ørskov, 1970).

3. Total endogenous loss of N, by extrapolation to zero intake, is proportional to $W^{0.75}$ (metabolic body weight) and is similar to the findings of Carr et al., (1975).

4. When N absorption was in excess of requirements, N retention was unaffected by N absorption, but linearly related to ME intake in fed animals of the same weight. Similar findings have been reported for milk fed calves (Blaxter and Wood, 1952). These results suggest that for ME intakes greater than those needed for positive N balance a constant proportion of ME intake is used in protein synthesis for animals of any given weight.

5. For animals receiving excessive nitrogen intakes and constant ME intake nitrogen retention decreased as body weight increased. This would indicate less of the energy available for growth was directed towards protein synthesis, and more was directed towards lipogenesis, as the animals became heavier. Graham and Searle (1972) in calorimetric studies with sheep and cattle found the fraction of energy storage that appears in protein decreases from 30-35% at low body weights to 10-15% in fully grown animals.

6. The relationship between N requirement/unit ME intake and intake ($ME/kg^{0.75}$) is curvilinear and asymptotic values which are a function of liveweight decrease as live weight increases.

Because of the large variation in the efficiency of utilization of ME in lambs and differences in the partitioning of ME used,

depending on cold stress, amount of exercise, and other factors and because overall predictions need to be applicable to ruminants N requirements are expressed in terms of NE (net energy) rather than ME, e.g.

$$\text{Total N requirement (g/d)} = aNE - bW^{0.75} - cW^{0.75} \text{ X NE} + d(W^{0.75})''$$

where a, b, c, and d are constants.

N requirement is usually multiplied by 6.25 and expressed as g reference protein/MJ ME intake in the diet. As stated earlier these relationships were developed for lambs but there appears no reason why these cannot be developed for calves.

Donnelly and Hutton (1976) working with pre-ruminant calves also used the technique of Hegsted (1964) as well as comparative slaughter to study the effects of differing levels of dietary protein and energy in growth. Feeding levels were adjusted to achieve two target rates of gain. The digestibility of DM was unaffected by protein conccentration, feeding level or age, whereas the digestibility of nitrogen increased curvilinearly with increasing dietary protein percentage. Similar results have been recorded by Roy et al. (1970), Raven (1972), and Lister and Lodge (1973). Both body weight and protein gains showed similar patterns of response to variations in protein and energy intake, but for maximum protein gain, protein requirements were higher than for maximum body weight gains. Multiple regressions were used to present the data similar to equations published by Andrews and Ørskov (1970a, 1970b) and Chiou and Jordan (1973) for similar conditions with the ruminant and pre ruminant lambs.

$$\text{Body weight gain} = aP - bP^2 + (cP \text{ X } DE) - d$$

(a, b, c and d are constants)

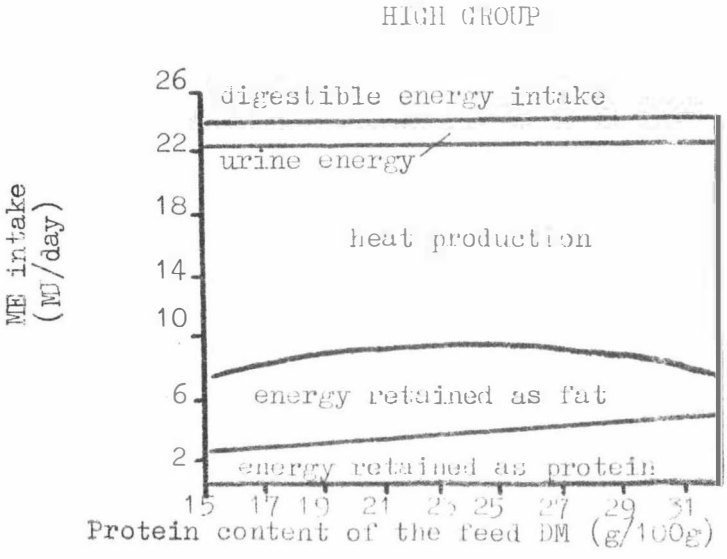
$$\text{Protein gain} = lP - mP^2 + nP \text{ X } DE - O$$

(l, m, n and O are constants).

DE = digestible energy intake (MJ/a) and P is percentage protein in the DM. With the increasing cost of protein components of feed, consideration of the above type of relationships when deriving rations may be of importance. For lean meat production, requirements for digestible protein could be based on desired protein gain.

Donnelly and Hutton (1976) presented the effect of protein level on energy utilization as a model. Fig. 2.4.

The relationship between daily energy intake and protein content of the feed. (From Donnelly and Hutton, pers. comm.)



Heat productions were highest for calves fed the diets of extreme protein content. Hartsook and Hershberger (1971) with rats, Walker and Norton (1971) with lambs, and Van Es et al. (1969) with calves, substantiate this finding. More fat was retained on the diets of low-mid protein concentration than those of higher protein content indicating preferential uses of energy for growth of lean body tissue, but where protein intake restricted this, the storage

of energy as fat. Andrews and Ørskov,(1960), Jagusch et al. (1970) and Norton et al. (1970) have previously altered the chemical composition of the bodies of preruminant and ruminants lambs by varying protein intake, while Bowman et al. (1965) found that by lowering the concentration of protein in the ration (of calves) the proportion of edible protein in the carcase is reduced and that of fat increased.

Bearing in mind the previous discussion it is virtually impossible to present protein requirements of young calves unless their age, liveweight, energy intake relative to that of protein, projected rate of gain (composition of gain) and physical environment are known. In Table 2.5 presentation of digestible nitrogen requirement of calves is accompanied where possible by its complementary input data. Parker and Hutton (1976) like previous workers with sheep (Andrews and Ørskov, 1970a, 1970b; Jagusch et al. 1970; Norton et al. (1970), noted the body compositional changes brought about by varying the protein : energy ratios and also accompanying changes in the utilization of both nutrients and stress the importance of the protein : energy interaction. The energy content of the digesta free body weight gained during the trial of Donnelly and Hutton (1976) decreased from 12.37 MJ/kg on the 16% protein diet to 9.31 MJ/kg on the 32% protein diet. This represents a change in energy storage as fat from 70% to 51% respectively. More detailed experiments incorporating slaughter techniques, the estimation methods of Hegsted (1964), realistic projected live weight gains, at varying intakes of different protein to energy ratios diets are needed before definitive protein requirements can be presented.

TABLE 2.5: Digestible N requirements of young calves.

Physical State	Projected LWG kg/day	Age	DMI g/kg$^{0.75}$	Energy Intake Digestible MJ/kg$^{0.75}$	Liveweight mean kg	Protein Digestible N requirement (g/d)	Measurement Technique - Comments and author
Ruminant	1.0	10-18 wks.	75-90	1.18 - 1.33	123	56	Stobo & Roy (1973) only 4 calves at 3 levels of protein NR versus ADN.
Ruminant	.75	8-12 wks.	88	1.19 - 1.21	64-68	C.P. 18.7g/kg DM	Stobo & Roy (1967) Liveweight and size basis 72 calves.
Ruminant	.65	-	86	1.10	100	45	NRC (1966) Feeding trials.
Ruminant	.55	-	78	0.99	75	28	Gardner (1968) Liveweight response feeding trials.
Ruminant	0.45	-	92	-	90	24	ARC (1965) Factorial approach
Non ruminant	0.61	2-9 wks.			40-70	27	Parker & Hutton (1976) - use of Hegsted (1964) retention versus intake approach. Also comparative slaughter.
	0.83	2-9 wks.		-	40-70	38	
Non ruminant	0.50			0.89	50	18	Jacobson (1969). Summary previous workers
Non ruminant	0.5			0.89	50	20	ARC (1965) (Factorial)
Non ruminant	0.80		69	1.27	40	33	NRC (1971)
Non ruminant	0.30		35	0.63	45	20	NRC (1971)

CHAPTER 3

MATERIALS AND METHODS

3.1 ANIMALS

Twelve Friesian bull calves were reared in pairs at the rate of one pair per week from mid March until the end of April on the Massey University town milk supply farm. Each calf remained three days on its mother and was then reared on whole milk to gain 0.5kg/day with pelleted concentrate being freely available throughout. In their third week the calves were moved to the Massey University Animal Physiology Unit.

3.2 LEVEL OF FEEDING

The experiment was designed so that the calves on a low level of intake (L)and a high level (H) would receive sufficient energy to allow for maintenance plus a 0.25kg/day and 0.75 kg/day liveweight gain respectively. Allowances in terms of ME were calculated using estimates for the ME value of milk as 2.82 MJ ME/kg and that for meal of 11.84 MJ ME/kg (Holmes and Davey, 1976) with an estimated cost of maintenance of 0.41 MJ ME/$kg^{0.75}$ (Davey, 1974). The energy costs per unit of LWG (live weight gain) 13.4 MJ ME/kg (H) and 11.4 MJ ME/kg (L) were also estimates from Holmes and Davey (1976).

3.3 GENERAL OUTLINE OF EXPERIMENT

The general outline is shown in Figure 3.1. The calves were randomly allocated to either a high or low level of intake calculated as above to allow the calves to gain 0.75 kg (H) or 0.25 kg (L) per day.

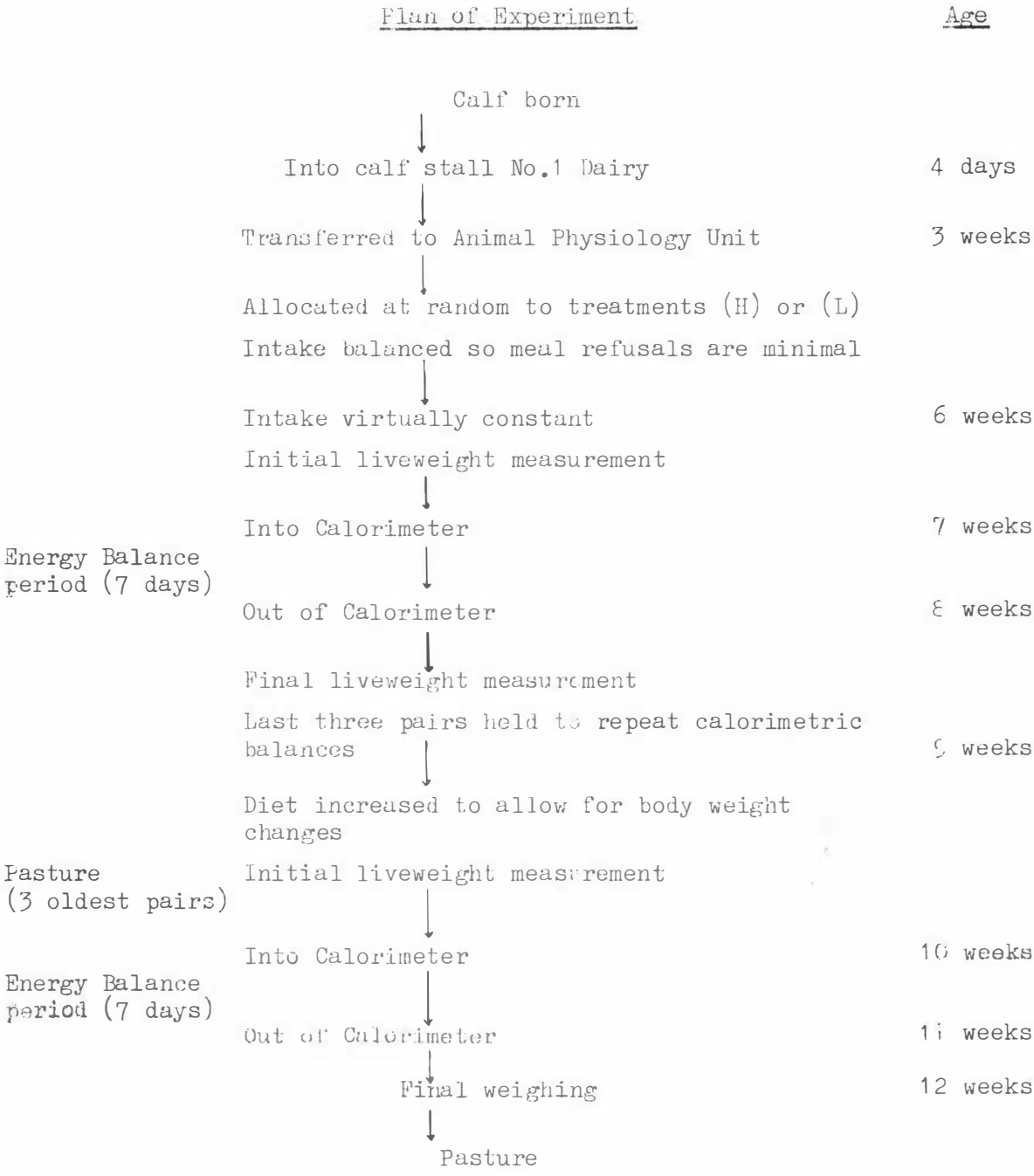


Fig. 3.1: Organisation of the experiment showing the average age in weeks of calves during each period of the experiment.

Once a calf was allocated to a high (H) or low (L) treatment it remained on this treatment even if undergoing a second balance.

3.4 FEEDS AND FEEDING

Quality of Feed

The calves were fed throughout the experiment on Friesian milk from the Massey No.1 Dairy Farm. Milk was collected daily at 8.00am., and when calves were in the calorimeter a separate consignment sufficient to last the calorimetric balance for each calf was collected at the start of the balance and stored in a chiller at $3^{o}C$.

Meal was provided by Northern Roller Mills in the pelleted form similar to proprietary weaning pellets marketed by this firm. Chemical composition was found to be as follows:

Material	Protein %	Fat % milk	Gross Energy
Milk (a)	3.36 ± .14	4.0 ± .10	3.08 ± 0.08
Pelleted concentrate (b)	18.32 ± 0.33		17.87 ± 0.49

(a) Estimates average over the nine calorimetric balance periods for liquid milk.

(b) Estimates presented per unit of DM.

Feeding

At the end of each week calves were weighed and their feed requirements determined for the following week on the basis of that liveweight unless they were in a balance period. Milk was weighed out in individual tared galvanised buckets for each calf and fed at 8.30am. each morning. Across the top of the feeding buckets a three inch wide strip of galvanised tin was welded to support

centrally a teat connected by clear plastic tubing to a unidirectional brass ball valve. This ensured that milk spillage from the calves mouth found its way back into the bucket. 10ml. of well mixed milk was sampled at each feeding for each calf undergoing calorimetric balances. All buckets were inserted in a large heated water bath so milk was approximately 38°C before feeding. Buckets and teats after completion of feeding were scrubbed in hot water containing a detergent and sanitiser and then rinsed and left to dry on a clean bench.

Prior to milk feeding, pellet refusals from the previous day (if any), were weighed and a subsample taken for dry matter (DM) determination. Pellets were then weighed into a tared bucket and added to each calf's individual bucket. Each day a handful of pellets was weighed out for DM determinations and another two handfuls were put aside to bulk for energy and protein determinations for the calves in the calorimeter. Clean water was available at all times.

Weighing

Calves were weighed on arrival at the Animal Physiology Unit and at weekly intervals thereafter. Weighing was done before feeding at 8.15am. on a portable Avery weighing platform accurate to 0.25 kg. Liveweight was measured over three weeks (including the balance period) in which dietary allowances were unaltered.

Calf health

Calves were kept under surveillance for scouring and any other outward signs of poor health.

Calf Housing and Calorimetry

All calves when not in the calorimeter were kept in metabolism crates in a controlled temperature room for the duration of the experiment. Ambient temperature was maintained at $17^{o}C \pm 1^{o}C$.

In the first balance one of two calves either a (H) or a (L) was assigned at random to calorimeter one its pair mate occupying calorimeter two. In any two successive balances in either calorimeter no two calves of a similar dietary treatment followed each other, i.e. H followed L or vice versa. This helped to randomize any uncorrected systematic errors, for example:

	Calorimeter 1	Calorimeter 1
Balance 1	Treatment H	Treatment L
Balance 2	Treatment L	Treatment H
Balance 3	Treatment H	Treatment L

3.5 Operation of the Calorimeters

Each calorimeter consisted of a chamber of galvanised sheet metal on a rigid steel framework 1.7m X 0.7m X 1.5m high (internal measurements), with a front and back door sealed by rubber gaskets. Both chambers were insulated with 2.5 cm. thick expanded polystyrene. The front doors of the chamber had built into them a feed and water trough which was accessible through a 0.3m. X 0.3m rubber sealed hatch. A perspex window protected by wire mesh in both back and front doors enabled the operator to inspect the animals within the chamber, however the animals within each chamber could not see each other.

The calculated volume of each calorimeter was 2,200 litres. The air temperature within the calorimeter was controlled at 18°C (± 1°C) by means of a water cooled heat exchanger and a thermostatically controlled electric heater mounted above a false ceiling beneath the top of the chamber. A small electric fan forced air through the air-conditioning unit concomitantly mixing the incoming air with that air already in the chamber.

Air was exhausted from each chamber, by two rotary vacuum pumps mounted in parallel, through a 2.5cm. diameter P.V.C. pipe set in the top of the rear door of the chamber. Fresh air was drawn from outside the building and entered the chamber through a 2.5cm. opening above the water trough in the front door of the chamber. Each calorimeter was operated at a pressure of about 2cm. water gauge below atmospheric pressure in a well ventilated, temperature-controlled room.

The exhausted air from each chamber passed through a device which cooled it to about 3°C, and then into a thermostatically controlled room at 28°C, ensuring that air was reheated to a constant temperature before being drawn through two dry gas meters connected in series. The air temperature was measured as it left the cooling device and again as it left the gas meters. As air was assumed to be saturated on leaving the air cooler an estimation of the water vapour pressure could be made. Barometric pressure was also recorded and with this and above data it was possible to correct the metered volume of air to conditions of S.T.P. (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 before it enters the chamber and the exhaust air on leaving the chambers. These air samples were dried in two separate 3m X 2.5cm. diameter silica gel columns. The system of solenoid valves

enabled exhaust air to be drawn alternatively from each calorimeter for four minute intervals, and fresh air for an eight minute interval every four hours. The resulting small samples were pumped through an automatic infra red carbon dioxide analyser (range 0 - 1.5% CO_2) and an automatic paramagnetic oxygen analyser (range 19-21% O_2) connected in series. The electrical output from each analyser was connected to a separate channel of a two-channel recorder (5 mv full range). The recorded traces for a twenty-one to twenty-three hour period could then be integrated manually with a travelling planimeter. This technique was rarely used as three spirometers with mercury-glass seals were filled daily by sucking air from the room, and the exhaust gas of the two calorimeters respectively through silica gel over a 21-23 hour period. A sample from each of these spirometers was then passed through the analysers in turn until the recorder trace steadied. Both gas analysers and the recorder were calibrated daily by pumping through them two different compressed gas mixtures of known composition.

Gas type (A) % O_2 20.801 % CO_2 1.199

Gas type (B) % O_2 19.617 % CO_2 0.709

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) as modified by the Royal Society of London (1972).

$HP = (O_2 \times 16.18) + (CO_2 \times 5.02) - (M \times 2.17) - (N \times 5.99)$

where HP = heat produced in (KJ) kilojoules/24 hr.

O_2 = volume of oxygen consumed in litres/24 hr. at STP

CO_2 = volume of carbon dioxide produced in litres/24 hr. at STP

M = volume of methane produced litres/24hr at STP

N = the mass of nitrogen simultaneously produced in the urine (g/24 hr)

An example of the calculation of heat production is shown in Appendix I.

Methane Determinations

Four days a week during calorimetric balances a 2.5 litre syringe was drawn off from the exhaust gas of each calorimeter which had been collected over a 23 hour period in a spirometer. This gas was taken to an infra red analyser set up to analyse methane at the D.S.I.R.

Tests applied to Calorimetric Equipment

The dry gas meters were tested against a spirometer (150 L) at the Palmerston North Gas Department Workshops, over the range of flow rates used in the experiment.

The whole apparatus was tested by the controlled burning of a weighed amount of absolute alcohol within the calorimeter for periods up to twelve hours duration. A series of such tests produced a mean measured O_2 consumption of 97.1% ($\pm$ 0.7%) of the theoretical oxygen consumption.

The calorimetric chamber, tested for air leaks by metering simultaneously the incoming and outgoing air, revealed a leakage of about + 3%, this representing a gain of air drawn into the system. No leaks were found between the chambers and the gas meters.

Collection of Faeces and Urine

The floor of each chamber was in the shape of a funnel so that urine which fell through the wire mesh on which the calf stood was collected in a plastic bucket containing approximately 2.5% (u/w) 0.1 N H_2SO_4 of the previous day's excreted urine. The urine was bulked over the week the animal was undergoing its calorimetric balance being stored at -3°C until the end of the week when it was thoroughly mixed and a subsample was taken for storage nitrogen and energy determinations.

Faeces were collected on a polythene sheet placed on the floor in the back half of the calorimeter and from the residue remaining when urine was strained. The daily collection during the calorimetric balance was bulked and stored at -3°C until the end of the balance when mixing subsampling and analysis took place. With healthy calves urine contamination by faeces was negligible.

3.6 TECHNIQUES OF ANALYSIS

Chemical Analysis

All chemical analyses were done in duplicate with discrepancies of greater than 3% requiring a repeat analysis.

Nitrogen Determination

The nitrogen contents of feeds and excreta was determined by the macro-Kjeldahl method (AOAC, 1965).

Bulk faecal samples at the end of each balance were weighed and then thoroughly mixed with a spade on a clean concrete floor. A sample was weighed out (~250g) and placed in an oven at 80°C for 48 hours to determine DM content. Another large sample was weighed, placed in a metal dish and freeze dried. The freeze dried sample was then ground

to a fine powder in a small "hammer mill". This powder was stored in screw top glass bottles for energy determinations. A further 1.0g subsample was placed in a plastic bag of known nitrogen content per gram and digested in the usual way. The pelleted concentrate was also ground, approximately one gram was placed in a small plastic bag of known nitrogen content this being digested in the normal way (AOAC, 1965). Both milk and urine were digested in liquid form.

Gross Energy Determinations

The gross energy of milk, concentrate, faeces and urine were determined in an Adiabatic Bomb Calorimeter. Samples of approximately a gram in the case of the faecal and concentrate powders were weighed into a plastic bag of know energy value and the total energy value was measured. Urine samples of 50.0ml. and milk samples of 5.0ml. were pipetted on to a polythene film (Gladwrap) in the bottom of a petri dish. The petri dishes were then placed in a freezer for a day and then freeze dried. The polythene film containing the solids was then combusted in a bomb calorimeter. Corrections were made for the energy value of the polythene, the specific gravity and H_2SO_4 content of the urine sample when calculating the total energy.

Statistical Analysis

The data derived on the high and low level of feeding for, intake of ME, heat produced, total energy retained, energy retained as fat and protein, nitrogen metabolism data and regression coefficients were subject to analysis of variance (Snedecor and Cochrane, 1973).

In addition simple and multiple regression analyses were performed with some of the data; the latter was carried out using the Burroughs Advanced Statistical Inquiry System programme.

Significance of differences

The following signs have been used throughout to describe the level of significance of differences between means

** Differences significant at the 1% level of probability

* Differences significant at the 5% level of probability

N.S. Differences not significant.

SE_m Standard error of mean.

A.O.V. Analysis of variance.

CHAPTER 4

RESULTS

General

The calves all settled quickly onto the prescribed treatment diets, with no obvious meal refusals. Adaption to the metabolism crates was also rapid and calves in the calorimeter appeared relaxed at all times.

4.1 Health

A single case of diarrhoea was recorded during one day in calorimetric period three for calf no. 2 on the (H) treatment. Kaolin was added to this calf's milk for the remainder of the balance period. Faeces and urine on the day of scouring were discarded, the calorimeter was scrubbed out and the collection of faeces and urine continued on the following day.

4.2 Liveweight

The mean values for liveweight and liveweight gain are presented in table 4.1; the values for liveweight gain were measured over a three week period which included the balance period in the second week; values for liveweight were those at the start of the balance periods (see materials and methods page 60).

Table 4.1

Liveweight and liveweight gain means for calves on treatments 'H' and 'L'

	Treatment		Results of analysis of variance	
	High	Low		
Liveweight (kg)	69.52±3.38	57.57±1.89	*	*
Liveweight gain (kg/day)	0.66±0.06	0.29±.06	*	*
Pooled mean Liveweight (kg)	63.54±2.38			

Differences between predicted (0.75 and 0.25kg/day) and actual gain are partly due to differences between the predicted and actual ME intake (see table 4.9).

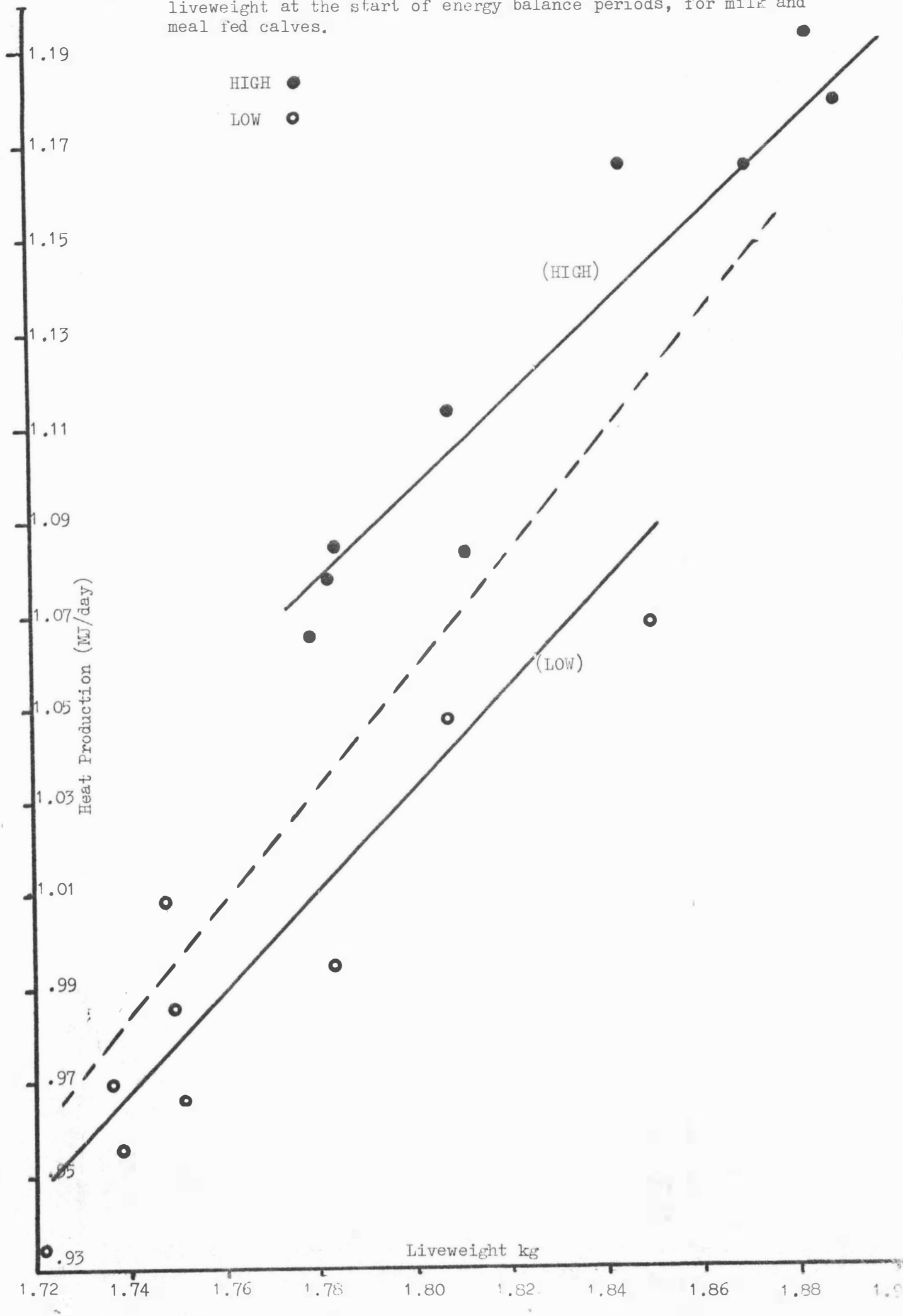
4.3 The relation between liveweight and energy balance data

The relations between $\log_{10}$ of heat production (the mean of seven days measurements) and $\log_{10}$ of liveweight were calculated for data from each treatment as well as for the pooled data.

The regression coefficients were 0.941 and 1.056 for the 'L' and 'H' calves respectively, the difference was not significant and the common regression coefficient was 0.980. (see appendix 2).

Despite the coefficient in this experiment being close to one, when Holmes and Davey (1976) analyzed their data

Fig.4.2: The relationship between heat production (mean of seven days) and liveweight at the start of energy balance periods, for milk and meal fed calves.



/kg$^{0.75}$ and /kg$^{1.0}$ there was little difference in results between both analyses, therefore for comparative purposes it was decided to use the conventional exponent 0.75 (Kleiber 1965).

Heat production was related to intake of ME see Fig. 4.3. In addition a multiple regression equation was calculated to relate HP to both LW$^{0.75}$ and level of ME intake. These equations along with those relating HP to LW have been presented in tables 4.2 and 4.3. The relations between $\log_{10}$ of ME intake and $\log_{10}$ of LW are also presented in table 4.2 .

Table 4.2

Regression equations relating heat production to liveweight and metabolizable energy intake to liveweight.

High level of intake (Treatment H)

$$HP = 0.249\ LW^{0.941}(\pm.112)$$

Low level of intake (Treatment L)

$$HP = 0.174\ LW^{1.056}(\pm.113)$$

Common regression coefficient

= 0.980 (see appendix 2).

(Pooled data) $HP = .200\ LW^{0.98}$

High level of intake (Treatment H)

$$ME = .760\ LW^{0.794}$$

Low level of intake (Treatment L)

$$ME = .095\ LW^{1.176}.$$

Common regression coefficient = 0.922 (see appendix 3).

(pooled data) $ME = 340\ LW^{.922}$

ME = metabolizable energy intake per day (mJ/day)

LW = Liveweight (kg)

HP = Heat production (mJ/day)

All equations significant $P < 0.01$.

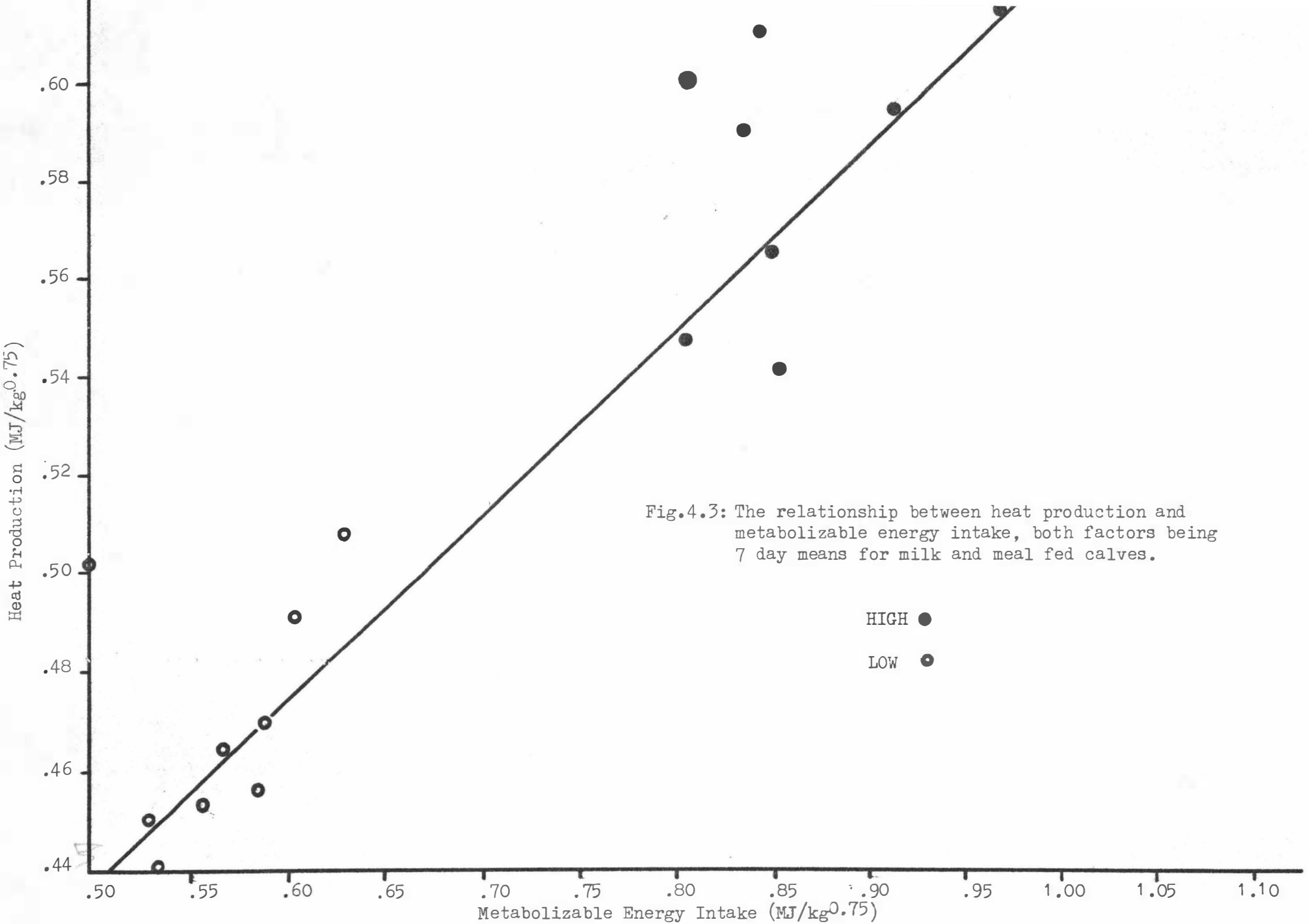


Fig.4.3: The relationship between heat production and metabolizable energy intake, both factors being 7 day means for milk and meal fed calves.

Table 4.3

Regression equations relating heat production to metabolizable energy intake and to liveweight

High level of intake

$$HP = 0.397 + 0.216\ ME\ (\pm 0.106)$$

Low level of intake

$$HP = 0.225 + 0.453\ ME\ (\pm 0.142)$$

The difference between regression coefficients of ME are N.S. so Pooled data

$$HP_{av} = 0.256 + 0.373\ ME\ (\pm 0.033)$$

HP = Heat production ($MJ/kg^{0.75}$)

ME = Metabolizable energy intake ($MJ/kg^{0.75}$)

Pooled data

$$HP_{av} = \underset{(\pm .105)}{0.272\ LW^{0.75}} + \underset{(\pm 0.052)}{0.422\ ME} - 1.203$$

HP_{av} = Heat production - average 7 days (MJ/day)

ME = Metabolized energy intake (MJ daily)

LW = Liveweight ($Kg^{0.75}$)

(All equations significant $P<0.01$)

Mean values for the several measurements of energy metabolism are presented in table4.4, along with estimates for energy retained as fat and as protein. The treatment H calves retained significantly more energy as fat than did the L calves (56% of 41%), however, the L calves retained more energy as protein 58% compared with 44% for the H calves. Both the H and L treatment calves converted gross energy (GE) to metabolizable energy with comparable efficiency.

Table 4.4

Mean values for energy metabolism and estimated values for energy retained as fat and as protein by calves receiving milk and meal

	Level of Feeding			Results of
$MJ/kg^{0.75}$	High	Low	SEM pooled	A.O.V.
Intake ME	0.882	0.569	±0.034	* *
Heat Produced	0.587	0.467	±0.009	* *
Energy Retained				
	(±0.024)	(±.006)		
Total	0.298	0.107	0.019	* *
as Fat	0.170	0.043	0.021	* *
as Protein	0.127	0.063	0.011	* *
ME/GE (%)	78.68	77.29	±1.231	N.S.

* * $P < 0.01$ * $P < 0.05$

Energy Retained	Feed Level			
	High Level	Low Level	SEM	A.O.V.
Fat/Total ER	0.561	0.413	.054	*
Pr/Total ER	0.438	0.584	.055	*

* $P < 0.05$

4.4 Utilization of metabolizable energy

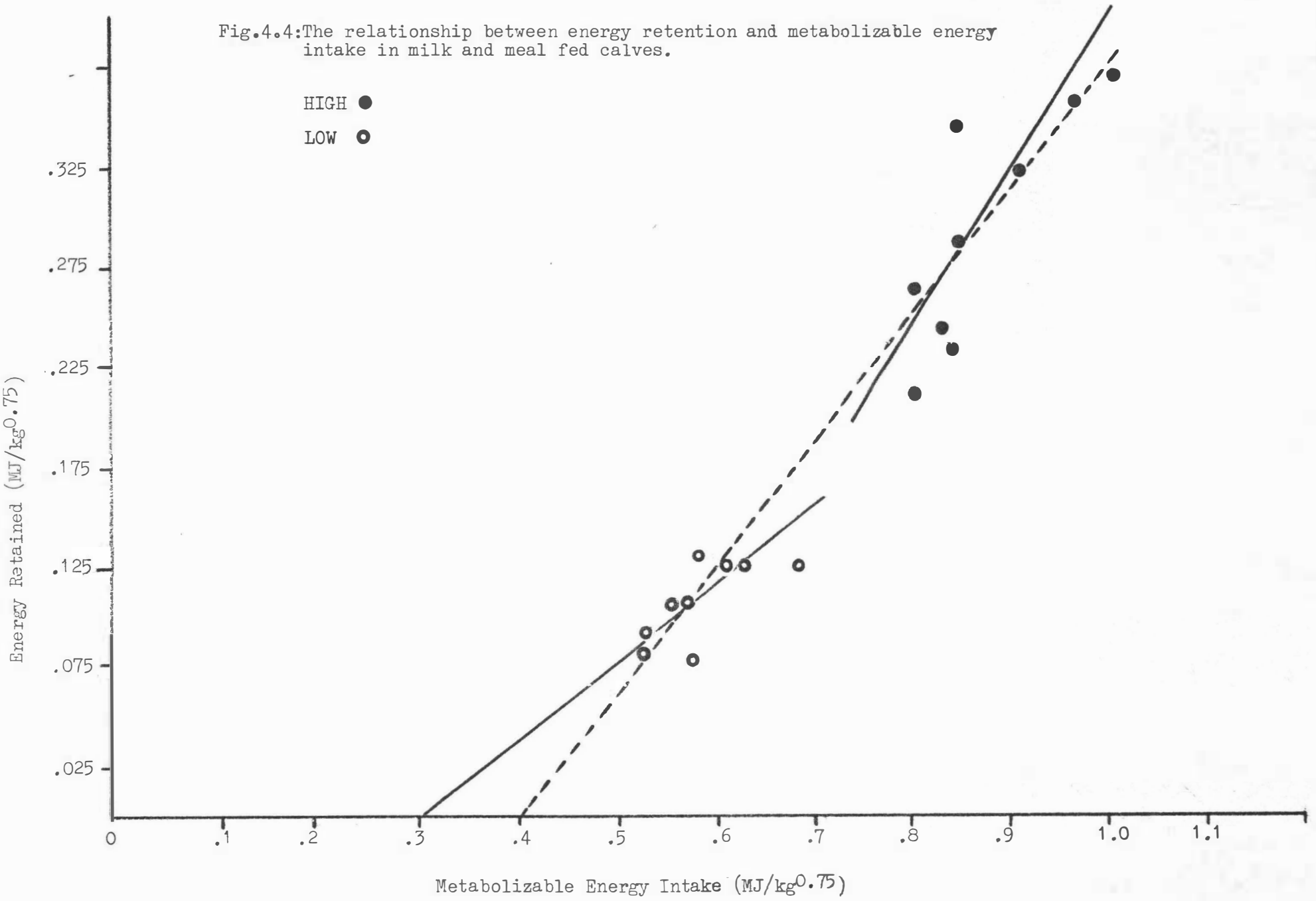
In order to obtain estimates of maintenance and K_g values, ER was regressed against ME intake. In addition ME intake was regressed against LW and either ER or ER as protein plus ER as fat. The ME value for maintenance is estimated when ER=0 for each equation. The values with the equations concerned are shown in table 4.5 .

Table 4.5

Regression Equations Relating Energy Retained Liveweight and Metabolizable Energy intake With Calves Receiving a milk meal diet.

Where: Y = ER $MJ/kg^{0.75}$ X=ME intake $MJ/kg^{0.75}$	Value for ME when ER=0 ($MJ/kg^{0.75}$daily)
(A) High level of Intake	
ER =.768 ME $(\pm.019)$ 0.379 ...(1)	0.493
Low Level of Intake	
ER = .402 ME $(\pm.147)$ 0.123 ...(2)	0.376
as the difference in coefficients of ME are N.S.	
Pooled Data	
ER = .634 ME $(\pm.042)$ 0.259	0.408
(B) MULTIPLE	
where Y = ME MJ daily	
X_1= LW $kg^{0.75}$	
X_2= ER MJ daily	
Pooled Data	
ME = 0.776 $LW^{0.75}$ + 1.309 ER - 6.897 $(\pm.077)$ $(\pm.075)$	0.471

Fig.4.4:The relationship between energy retention and metabolizable energy intake in milk and meal fed calves.



(C)

where Y = ME MJ daily

X_1 = $LW^{0.75}$ (kg)

X_2 = ER_p (protein) MJ daily

X_3 = ER_c (fat) MJ daily

Pooled Data

$$ME = \underset{(\pm.082)}{.608\ LW^{0.75}} + \underset{(\pm.209)}{2.232\ ER_p} + \underset{\pm(.123)}{1.00ER_F} - 4.407 \quad .413(ME_m)$$

(D) where Y = ME $MJ/kg^{0.75}$ daily

X_1 = ER_p $MJ/kg^{0.75}$ daily

X_2 = ER_F $MJ/kg^{0.75}$ daily

Pooled Data

$$ME = \underset{(\pm.136)}{0.940\ ER_F} + \underset{(\pm.279)}{2.665\ ER_p} + 0.374 \qquad 0.374\,(ME_m)$$

All equations significant ($P < 0.01$)

The regression of the pooled data of ME intake versus energy retention is shown in figure 4.4 . The variation in maintenance levels of ME calculated from the multiple regressions versus the linear regression may be due partly to high correlations between supposedly independent variables used in deriving the multiple regressions.

4.5 Nitrogen Metabolism

The mean values for measurements of nitrogen metabolism have been presented in table 4.6 and figure 4.5.

Fig.4.5The relationship between nitrogen retention and nitrogen intake for calves on a milk and meal diet.

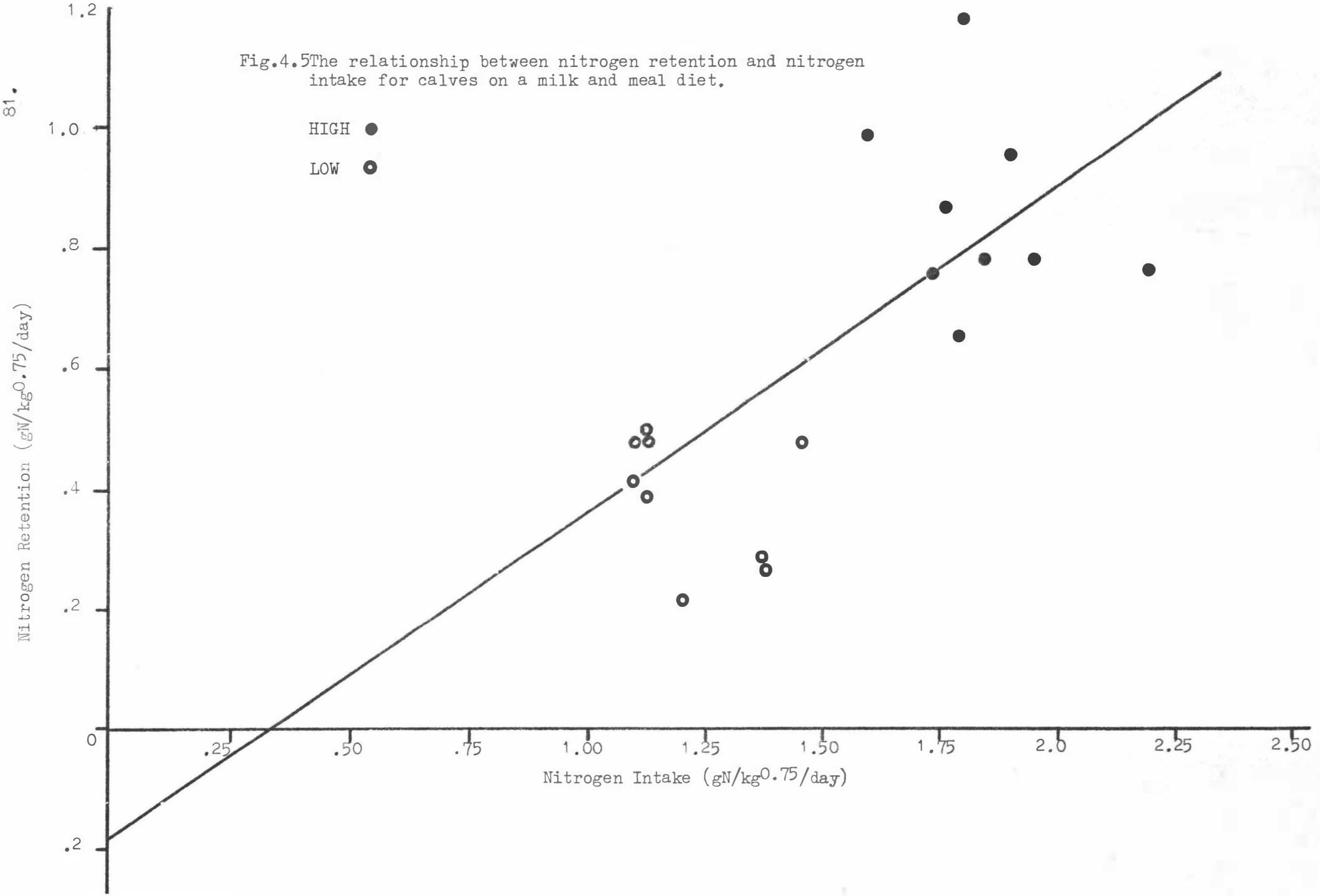


Table 4.6

Mean values for nitrogen metabolism of calves receiving a milk meal diet.

	Level of feed		
($g\ N/kg^{0.75}$ daily)	High	Low	A.O.V.
Total N intake	1.839 (±.054)	1.23(±.042)	* *
N intake meal	1.016±.066	.660±.036	* *
N intake milk	.824±.058	.553±.034	* *
Digested N intake	1.519(.052)	0.962(±.033)	* *
Urine N	0.666(.023)	0.563(.027)	*
N retained	0.854(.053)	0.398(.046)	* *
DN/GN x100(%)	0.825(.005)	0.793(.008)	* *

Figures in brackets SEM - standard errors of means

* Treatment effect significant $P < 0.05$

* * Treatment effect significant $P < 0.01$

4.6 Energy Retained in Relation to rate of gain in Liveweight

Using values for liveweight gain (mean over three weeks) and ER measured over the week long calorimetric balance it was possible to estimate the amount of energy retained per Kg of liveweight gain; these have been presented in table 4.7. and Figure 4.6 .

Fig.4.6:The relationship between Energy Retention and Liveweight Gain, (the mean of three weeks).

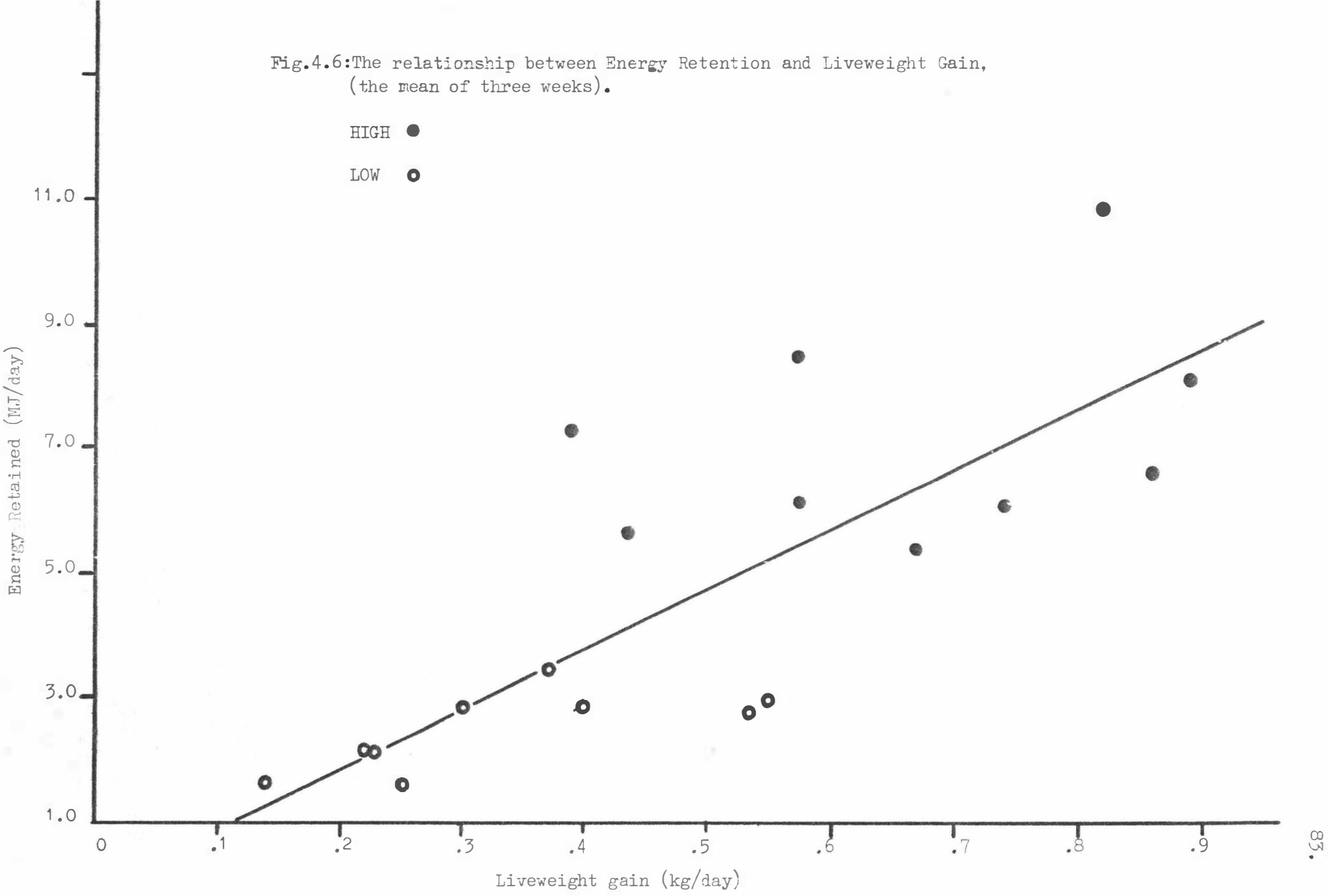


Table 4.7

Regression Equation Relating Energy Retained with liveweight gain.

ER = MJ/day

LWG = Kg/day

Pooled data

$$ER = 9.383\ (\pm 0.642)\ LWG - 0.248\ **$$

Energy retained per Kg Liveweight gain for calves receiving milk and meal

	Level of feeding		
MJ's energy retained/kgLWG	HIGH	LOW	Analysis of variance
(mean)	10.43	8.102	NS
(range)	(7.55-13.18)	(5.02-9.42)	($P < 0.05$)

There is considerable variation within each treatment mean. There was no significant difference between the two levels of feeding in energy retained per kg.

4.7 Methane values

The mean values for methane production are shown below in Table 4.8.

Table 4.8. Methane production in Litres/day

	Treatments		Analysis of variance
	High	Low	
Methane produced ($L_{/day}$)	8.9±1.0	4.2±0.6	* *

The energy lost as methane by the calves on the 'L' and 'H'

Treatments were 0.79% of GE (Gross energy) and .65%

Table 4.9 . mean values for energy and nitrogen metabolism of calves for the two treatments

(all units MJ/Kg$^{0.75}$) unless stated otherwise	High	Low
ME intake	0.882	0.569
Heat produced	0.587	0.467
Energy retained	0.298	0.107
Total N intake (g/kg$^{0.75}$)	1.839	1.213
Digested N (g/kg$^{0.75}$)	1.519	0.962
N retained (g/kg$^{0.75}$)	0.854	0.398
Liveweight gain (kg/day)	0.66	0.29
	Meal	Milk
Predicted GE intake	19.74MJ/Kg	2.98MJ/Kg
Actual GE intake	17.91MJ/Kg	3.16MJ/Kg

CHAPTER 5

DISCUSSION

All calves appeared to be in good health apart from one case of diarrhoea as reported in the Results Section.

5.1 Liveweight gain

The difference between the predicted and the actual liveweight gain as depicted in Table 4.9 can in part be attributed to the difference between the actual and the predicted GE intake.

5.2 Energy

Intakes and the plan of the experiment are dealt with in the Materials and Methods Section (see Fig. 3.1). The metabolizability of the milk meal diet in the present study 0.78 is lower than that reported by Holmes and Davey (1976) for milk fed calves (.95), but considerably higher than values reported for maturing ruminants on solid diets 0.58 and 0.60, Blaxter et al. (1966), Neergaard (1974). The factor for converting DE to ME in this present study 0.94, is considerably higher than values reported by Blaxter et al. (1966) 0.82 and Neergaard (1974) 0.84 for maturing ruminants where methane losses were 9 and 7% of gross energy respectively, considerably higher than the 1% in the present case. This suggests that while the rumen may be functional (Lengemann and Allen, 1959) normal microbial populations do not become fully developed for several months, particularly in this case where there was minimal contact with mature ruminants (Preston and Willis, 1974).

1. The Exponent of Liveweight

The relationship between heat production and body weight, and between metabolizable energy intake and body weight are presented in Tables 4.2 and 4.3 respectively. The relationship between food intake and liveweight would appear to influence the relationship between heat production and liveweight. Present results and those of other workers are summarised below:

Food intake	(kg) Body weight	Exponent	Animal	Source
$W^{1.0}$	34-64	0.8	Pigs	Holmes & Mount (1967)
ad libitum	20-45	0.9	Pigs	Mount & Holmes (1967)
$W^{1.0}$	17-34	1.0	Pigs	Holmes and Mount (1967)
$W^{.92}$	50-90	.98	Calves	Present study

As mentioned earlier in the Results Section (see page 75) the present data was analysed using an exponent of 0.75 (Kleiber, 1965 and 1969).

2. Maintenance and net efficiency of utilization of ME above maintenance (kg)

The regression equations, both simple and multiple, from which estimates of ME_m (metabolizable energy required for maintenance) were calculated are shown in Table 4.5. The relationship between energy retained and ME intake both expressed per $kg^{0.75}$ is shown in Fig. 4.4. This graphical depiction is a good example of the danger of extrapolating from a narrow range of results when estimating ME_m (Van Es, 1972). The regression lines for both the (H) and (L) treatments when extrapolated to zero energy retention would give

estimates of ME_m varying widely from that obtained with the pooled data.

As both intake (MJ ME/$kg^{0.75}$/day) and liveweight ($kg^{0.75}$) differ significantly between treatments, the multiple regression analysis used in the determination of the energy cost of fat and protein deposition has been presented in two forms (see Table 4.5). Equation D from Table 4.5 encompasses an exponent of liveweight ($kg^{0.75}$) in both the dependent and independent variables similar to equations presented by Rattray and Joyce (1976). The resulting estimates of ME_m 0.47 (equation B) and 0.37 MJ ME/$kg^{0.75}$/day (Equation D) highlight the difference in results from the two analysis techniques. Little confidence is placed on the estimate 0.47 MJ ME/$kg^{0.75}$/d because of the failure of the analysis technique used to account for differences in liveweight and intake between treatments. The estimate of ME_m 0.41 MJ ME/$kg^{0.75}$ from equation C is also discounted for similar reasons.

The present estimate of ME_m, 0.41 MJ ME/$kg^{0.75}$ per day for the pooled data (Table 4.5A) and the range 0.37 and 0.41 MJ/$kg^{0.75}$ (also Table 4.5 A, D) are similar to the recently published values of Johnson and Elliott (1972a and b), Van Es *et al*. (1969), Holmes and Davey (1976), Vermorel *et al*. (1974) for milk or milk substitute fed calves and those calculated from the data of Neergaard (1974) for young ruminant calves (see Table 2.3). In view of the similarity between all of the above estimates the recently reported value of 0.68 MJ/$kg^{0.75}$/d (Webster, Gordon and Smith, 1976) for veal calves is difficult to explain. Errors in technique are unlikely because excellent agreement was obtained between the results of direct and indirect calorimetry. Differences because of the very high intake of Webster's calves can be discounted as the relationship between

ME intake and heat production was linear. The slightly higher value for kg reported by these workers would account for only a small part of the difference in ME_m. In Webster's work the calves were changed between the different treatments (different energy intakes) in a random fashion whereas in the present experiment calves remained on the same treatment for both energy balances. However Holmes and Davey (1976) switched their calves between high and low or low and high in subsequent balances and Van Es et al. (1969) used both types of experimental design in their pooled data and as their estimate of ME_m along with that of Holmes and Davey (1976) and the present study are very similar, differences due to the design of the experiment are likely to be quite small. This leaves as the only obvious remaining factor, possible differences in activity, or tension because of isolation or method of handling. In the present experiment day to day variations in heat production during the seven day measurement period were very small (pooled SEM = $\pm$ .18 MJ/day) indicating that the animals were relaxed within their new environment. As isolation per se has been shown to have no effect on the heat production of young lambs (Webster, Smith and Brockway, 1972) it is very difficult to see how measurable differences in activity or state of vigilance attributable to isolation could account for the magnitude of the difference between the results of Webster et al. (1976) and other workers. However in a later paper (Webster, Smith and Mollison, 1976) Webster accounts for the difference by introducing the term he calls "impetus for growth" which determines heat production at a particular combination of body weight and ME intake. This "impetus for growth" apparently is related to sex, breed, stage of maturity and prior nutrition, but

why it should only effect Webster's calves and not those of Van Es *et al.* (1969) or Vermorel *et al.* (1974) whose calves were of a similar age, sex, breed, stage of maturity, prior nutrition, and rate of growth remains uncertain.

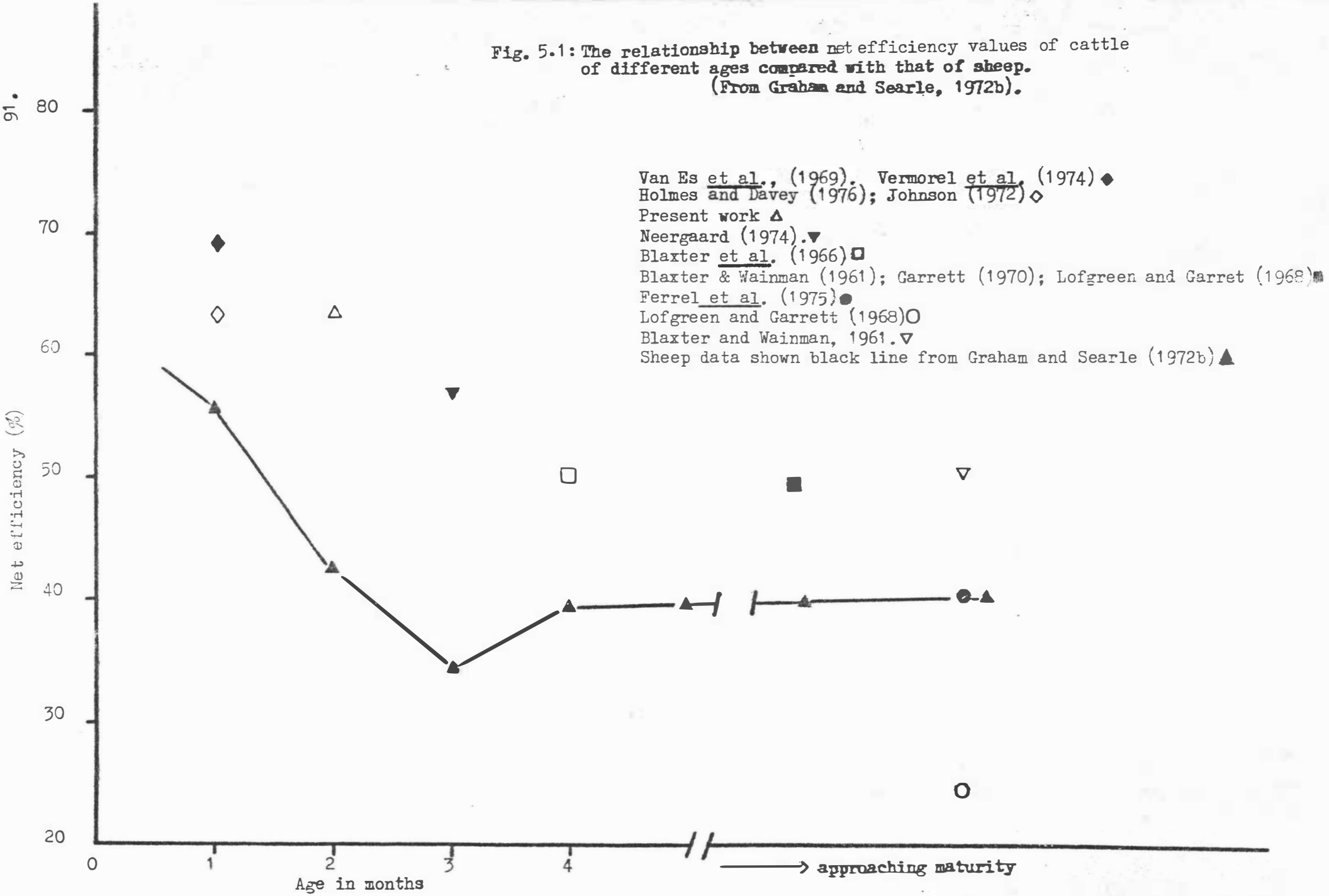
The net efficiency of utilization of ME above maintenance (kg) 0.63 is the same as the value reported by Holmes and Davey (1976) for their Friesian milk fed calves and similar to values reported by Van Es *et al.* (1969), Johnson and Elliott (1972a, b), Webster *et al.* (1976) and Vermorel *et al.* (1974). It is however somewhat higher than the values reported by Neergaard (1974) and Blaxter *et al.* (1966) as shown in Table 2.4 for older, heavier and fully ruminant calves, fed solely on a solid diet.

Values for net efficiency of the "transitional ruminant" calf when inserted between those of the pre-ruminant and ruminant (see Table 2.4) present a similar pattern to that reported for sheep by Graham and Searle (1972) (see Fig. 5.1). These workers noted a decrease in net efficiency with rumen development, stabilizing as the rumen became fully functional.

3. The Energy Cost of Fat and Protein Deposition

The values derived from the present data (Table 4.5D) for the efficiency of utilization of ME for the formation of fat and protein 1.00 MJ ME/MJ fat and 2.66 MJ ME/MJ protein correspond to partial efficiencies of 1.00 and 0.38 respectively. However when independent variables are highly correlated as in the present case (protein and fat were correlated with ME intake with 'r' values of .92 and .95 respectively and with each other with an 'r' value of 0.82) a multiple regression is not a good model to fit (Rattray and Joyce, 1976; Ørskov and

Fig. 5.1: The relationship between net efficiency values of cattle of different ages compared with that of sheep. (From Graham and Searle, 1972b).



McDonald, 1970; Buttery and Boorman, 1976). Most estimates of energy cost for protein and fat deposition quoted in the recent literature (see Table 2.2) are determined by comparative slaughter techniques as energy balance trial techniques often over-estimate energy and nitrogen retention. It appears however that the correlation among so called independent variables is no greater in the present case than that in the data used by other authors (see Rattray and Joyce, 1976; Holmes and Davey, 1976). The pooled value for the partial net efficiency of utilization of ME for the synthesis of protein 0.38 is somewhat lower than that reported by Osinska (1974) of 0.41 (assuming a protein energy value of 23.3 MJ/kg), Holmes and Davey (1976) of 0.54 but higher than the value of Donnelly (1975) of 0.36 (see Table 2.2). Apart from the difference between the present value and that of Donnelly's the present results appear to confirm the findings of Kielanowski (1976a) and Rattray and Joyce (1976) that ruminant protein deposition is much less efficient than in pre-ruminants, or non ruminants (see Table 2.2) Rattray and Joyce (1976) propose possible reasons for this difference:

1. Inefficiencies due to costs of rumen fermentation (Blaxter et al., 1966).

2. Deamination of dietary amino acids (Clark, 1974).

3. Absorbed end products of ruminant digestion may be used inefficiently for protein synthesis (Eskeland et al., 1974).

4. High turnover of ruminal epithelium with subsequent losses of N lowering net protein compared with pre-ruminants or other species.

The partial efficiency of utilization of ME for the formation of fat is 1.0 the same as reported by Donnelly (1975) and similar to Holmes and Davey (1976).

In the light of the recent papers by Kielanowski (1976a, b) and the model approaches presented, it seems likely that accurate estimates of the energy cost of protein and fat deposition, maintenance, lean body mass to protein, feed conversion efficiency and LWG may one day enable nutritionists to calculate the total daily gains of protein and fat independently of one another and enable selection on the basis of protein gain from a measure of LWG and feed conversion efficiency alone. Work by Carr and Brookes (pers. comm.) to establish relationships between maximum levels of nitrogen retention for differeing levels of ME intake to obtain different projected liveweight gains over differing weight ranges in calves will add another dimension to the modelling concept proposed by Kielanowski (1976b) and will possibly enable empirical relationships to be evolved.

4. Energy retained per unit of Liveweight Gain

The values derived from the present data for energy retained per kg liveweight gain (LWG) (see Table 4.7 and Fig. 4.6) are quite variable, however the mean value 9.38 MJ/kg is similar to that of Holmes and Davey (1976) for Friesian calves, Johnson and Elliott (1972a, b) for Friesland calves and values presented by the Agricultural Research Council (1965). The value of Joyce et al. (1975) for the grazed and stall fed cattle of 40 MJ ME/kg (LWG) when converted to a net energy cost assuming K_g = .40 becomes approximately 16 MJ/kg LWG or 60% higher than the present estimate. The mean value from the present results can be converted to ME required per kg LWG by multiplying by the pooled value for K_g of 0.63, giving a range of values from 12.85 to 16.53 MJ ME/kg LWG for the low and high levels

of feeding respectively. In light of the findings by Donnelly and Hutton (1976), Johnson (1972), Liebenberg and Mercoe (1974, 1975) in which body composition of calves was shown to be altered by nutrition, the body compositional changes with increasing weight and age (A.R.C., 1965; Lofgreen and Garrett, 1968; Blaxter et al. 1966) and the different energy densities of fat and protein (Buttery and Boorman, 1976; Kielanowski, 1976a), the above results are only applicable to the diet and conditions under which it was fed.

5.3 'True' Net Energy Maintenance

When ME intake is at maintenance, or below, the heat produced by an animal can be divided into two components:

1. That which might be termed the 'true' net energy cost of the processes involved in maintenance;

2. That which is produced during the conversion of dietary ME and/or body energy stored to the 'true' net energy required for maintenance.

Obviously 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 connected with the formation of ATP. It may however be possible to accomplish the partitioning statistically as proposed by Kielanowski (1976) or assumed by Lofgreen and Garrett (1968). Kielanowski (1972) argues that that portion of HP (heat production) proportional to energy intake corresponds to the energy liberated during the synthesis of ATP, while HP connected with true net energy cost of maintenance is independent of energy intake. Therefore the constant term in the

pooled regression in Table 4.3 (0.26) represents an estimate of "true" NE_m. Because of the relationship between ME intake HP and energy retained (ER) it may also be argued that the constant regression term in the regression equation relating ER to ME intake as shown in Table 4.5A also represents an estimate of true NE_m.

Armstrong (1969) reviewing theoretical attempts which estimated true k_m, calculated 0.63 to be an average value in the literature for a wide range of diets. Using this theoretical net efficiency value and the present pooled value for ME_m 0.41 $MJ/kg^{0.75}/d$ (see Table 4.5A) an estimate of true net energy required for maintenance (NE_m) of 0.26 $MJ/kg^{0.75}$ daily is obtained.

Presented below is a Table of estimated "true" NE_m values from the literature.

Source	Net Energy Maintenance $MJ/kg^{0.75}/d$	Comments
Holmes & Davey	0.25	Pre-ruminant calves
Van Es *et al.* (1969)	0.29	Veal calves
Lofgreen & Garrett (1968)	0.32	All sexes, differing diets, all ages. (cattle)
Present study (1976)	0.26	
Garrett (1974)	0.31	(230-400kg) male and female cattle.
Blaxter *et al.* (1966)	0.29	15-81 week old cattle
Webster *et al.* (1976)	0.47	Veal calves
Kielanowski (1972)	0.25	Pigs 20-90 kg
Walker & Norton (1970)	0.25	Sheep pre-ruminant

Alternatively if FHP is assumed to be constant at approximately 0.42 $MJ/kg^{0.75}$ daily (Blaxter *et al.*, 1966; Holmes and Davey, 1976;

Webster et al., 1974) and 'true' NE_m is 0.26 (value from present study) then the corresponding 'true' k_m would be 0.62 which is quite close to the theoretical value proposed by Armstrong (1969). It is also of interest to note the similarity between Armstrong's theoretical k_m (0.63), the 'true' k_m as calculated above (0.62) and the net efficiency of utilization of ME above maintenance K_f (0.63) in this present study.

The only estimate of 'true' net energy maintenance at wide variance with values listed in the Table above is that of Webster et al. (1976). The remainder of the values are reasonably close to the value of 0.32 $MJ/kg^{0.75}$/day taken by Lofgreen and Garrett (1968) as a constant NE_m for all diets, ages and sexes of cattle which is used as a basis for estimating NE_m values of foods in the N.R.C. (1970) feed requirement system. In contrast estimation of maintenance costs in the ARC (1965) system is based on measurements of FHP. Such an approach is open to doubt because of the variability in FHP which is influenced by many factors as mentioned in the Literature Review (see page 36).

Graham et al. (1974) have presented data for lambs which would enable a "standardized" FHP to be calculated, while Webster et al. (1974) (1976) have produced an empirical relationship ("the U.K. System") that estimates predicted FHP, F in an endeavour to reduce the variation in measurements of FHP. The approach of Graham et al. (1974) would appear to be the more soundly based since Webster's "U.K. system" depends on two empirical relationships which may confuse the issue even more.

Nitrogen Metabolism

The calves on the H treatment appeared to retain less energy as protein than those on the L treatment the difference being significant (see Table 4.4). The graph of nitrogen retention (NR) versus nitrogen intake (NI) is shown in Figure 4.5. From the extrapolation to zero nitrogen retention, nitrogen required for maintenance (N_m) was 0.35 gN/$kg^{0.75}$/day or 0.28 g Dig N/$kg^{0.75}$/day. This value is comparable with those reported for ruminating calves 0.33 and 0.27 g Dig N/$kg^{0.75}$/day (Stobo and Roy, 1973) but it is hard to imagine that the absorbed amino acids available for tissue synthesis is the same in both cases. The obligatory N losses in the present work calculated by extrapolating the regression of NR versus NI to zero nitrogen intake were 0.19 gN/$kg^{0.75}$/day. The biological value for the mixed diet was 0.53. Because of the lack of points about and below maintenance (see Fig. 4.5) and the findings of Carr (pers. comm.) that the slope of the line below maintenance is not the same as that above little emphasis has been placed on the above results.

Since both Nm (Carr et al., pers. comm) and MEm (Blaxter et al., 1966) are apparently proportional to metabolic body size, the amount of protein : energy (CP : ME) in the diet may be taken as a constant with age or weight (CP : N X 6.25). The value for the present data is 5.35 g N/MJ ME for the milk meal diet in question.

Methane

Judging from the values for methane production cited for ruminant calves (up to 15 weeks old) by Neergaard (1970, 1974) and Blaxter et al. (1966) of 9 and 7% of gross energy intake respectively, the

rumens of the calves in the present experiment were far from fully developed, while the measured methane production would suggest the rumen was functional (Lengemann and Allen, 1959) the type of microbial population established may not be that of the mature ruminant, especially in the present case where calves apart from at birth, had no contact with mature ruminants (Preston and Willis, 1974).

Practical implications

As a result of the present study the following Table of requirements at various weights and growth rates has been compiled.

Table 5.1: Requirement for Friesian calves on milk and meal diets for varying body weights and liveweight gains (all units in kg's.)

Weight of calf	Growth Rate (kg's/day)							
	0.25		.5		.75		1.0	
	Milk	Meal	Milk	Meal	Milk	Meal	Milk	Meal
50 *	2.5	.44	3.3	.58	4.1	.72	4.9	.86
75 *	3.0	.54	3.8	.68	4.7	.82	5.5	.96
100 *	3.6	.63	4.4	.77	5.2	.92	6.0	1.05

* assumptions : maintenance = .41 MJ/$kg^{0.75}$

Energy reqd./LWG = 15 MJ ME/$kg^{0.75}$

Gross energy milk 3.0 MJ/kg (Friesian milk)

Pelleted concentrate 17.0 MJ/kg (19% crude protein)

Metabolizability of the diet = .78

50% of ME from milk the other 50% of ME from meal.

The energy required per unit liveweight gain is accurate for the conditions of this experiment between 50 and 75 kg but will probably increase again between 75 and 100 kg. liveweight because of body

compositional changes with growth (Blaxter et al., 1966) The metabolizability of the diet did not appear to decrease at the higher levels of intake which supports the finding of Webster et al. (1974) for low fibre concentrate diets. It should be remembered that values for maintenance and energy requirements per unit LWG were obtained in calorimeters in which temperature, humidity and activity were controlled so allowances according to the amount of activity (see A.R.C. 1965) and local environment (Holmes and McLean, 1975) would have to be added to the above values.

Conclusion

The energy metabolism of Friesian calves receiving half their ME intake from concentrate and half from milk is similar to that of pre-ruminant calves (Holmes and Davey, 1976; Vermorel et al. 1974 and Johnson, 1972). The energy costs of protein and fat deposition in the present study are also very close to values presented by Donelly (1974), Osinska (1974) and Holmes and Davey (1976). Rattray and Jagusch (1977) noted that the energy cost of protein deposition decreased markedly for sheep receiving milk, compared with those receiving pasture.

It seems likely that the higher K_g value for calves fed concentrate and milk compared with those receiving concentrate and roughage is due to the energy cost of protein deposition. It may be possible to increase the net efficiency of energy utilization of young calves receiving concentrate by including a small proportion of milk in the diet.

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Appendix One

Calculation of Heat Production from Raw Calorimetric Data

Calf : 14

Date : 30.5.75

Atmospheric pressure 766mm

Cooler temperature 10.4°C saturated WVP of 10mm)

meter-room temperature 24.3°C

Measured air flow rate 43.65 L/min

Flow through analysers 543L/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	94 (20.95%)*	45(19.92 (a)	49 (1.03%)
Finish of measurement	99 (20.95%)*	59(19.60)	40 (1.35)

* The 20.95% value is the almost standard value for normalair

(a) 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) = 51.0 divisions.

The number of chart divisions between incoming and outgoing CO_2 - (measured from spirometer aliquots) = 55.8 divisions

Urinary nitrogen (g) = 15.91g/day

Calibration of analyser with reference gases

Reference Gas	CO_2 Known %	CO_2 Reading in chart divisions	O_2 Known%	O_2 Readings in chart divisions
Bottle A	1.199	74.9	20.801	70.7
Bottle B	0.709	56.9	19.617	19.1
purge		18.9		77.3
(Atmospheric air)				

(A-B) O_2 = 51.6 divisions

50% O_2 per division $= {}^{1.184}/_{51.6} = 0.0229\%$

Flow rate corrected to S.T.P.

Correction factor = $(766-10)/760 \times 273/(273+24.3) = .913$

Total Ventilation Rate

Since 1440 minutes/day

average rate = (1440x43.65) + flow through analyser (543 L/day)

= 63399 L/day

Correcting to STP 63399 x .913

= 57883 L/day

Volume of Oxygen Consumed

1 chart division = .0229% O_2

51 divisions = 51.0 x .0229 = 1.168

Volume of O_2 consumed = $57883 \times 1.168/100 = 676.07$

= 676.07 L/day

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

$= (-9 \times .0229/100 \times 2.200)$

= -4.534 L/day

Correcting volume of O_2 consumed

= 676.07 - 4.534

= 671.54 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 55.8 divisions corresponded to a percentage CO_2 reading of 1.10%

Thus RQ = $CO_2 / O_2 = 1.10/1.168 = 0.942$

0.942 x corrected O_2 consumption = CO_2 consumption

= 0.942 x 671.54 = 632.59

= 632.95 L/min

Volume of CH_4 produced

% CH_4 in air leaving calorimeter minus % CH_4 in air entering = 0.019

volume of CH_4 = $0.019/100$ x 57883 = 10.00 L/day

Daily Heat production

$HP = (O_2 x 16.18) + (CO_2 x 5.02) - (M x 2.17) - (N x 5.99)$

$HP = (671.54 x 16.18) + (632.95 x 5.02) - (10 x 2.17) - (15.91 x 5.99)$

= 13,925MJ/day or 13.93 MJ/day

Appendix Two

Test of the probability that the two regressions relating heat production to liveweight did not come from the same population.

Analysis of Variance

						Deviations from Regression		
Group	d.f.	Sx^2	Sxy	Sy^2	b	SS	d.f.	MS
High (H)	8	.034	.032	.033	0.941	.003	7	.0004
Low (L)	8	.018	.019	.027	1.056	.007	7	.001
Common Regression	16	.052	.051	.060	0.980	.010	14	.0007

Source of variation	d.f.	s.s.	M.S.
Error for unadjusted means	16	.060	
Reduction due to regression	1	.050	
Error (difference)	15	.010	

Source of variation	d.f.	s.s.	M.S.
SS for deviations from common regression	15	.010	
SS for deviations from individual "	14	.010	.0007
Error	1	0	

F (1,14) .NS

using Y = MX+b (eqn for linear regression) mean values of HP and LW (both expressed in Logs) and a common regression coefficient of 0.980 derived equations for the data were

High (H) $HP = .214\ LW^{0.980}$

Low (L) $HP = .187\ LW^{0.980}$

(Pooled data) $HP = .200\ LW^{0.980}$

Appendix Three

Test of the probability that the two regressions relating ME intake to liveweight did not come from the same population

Analysis of Variance

Group	d.f.	Sx^2	Sxy	Sy^2	b	Deviations from Regression S.S.	d.f.	M.S.
High (H)	8	.034	.027	.033	.794	.021	7	
Low (L)	7	.017	.020	.028	1.176	.004	6	
Common Regression	15	.051	.047	.061	0.922	.016	13	

Source of variation	d.f.	s.s.
Error for unadjusted means	15	.061
Reduction due to regression	1	.043
Error (difference)	14	.018

Source of variation	d.f.	s.s.	M.S.
SS for deviations from common regression	14	.018	
SS for deviations from individual regression	13	.016	.001
Error	1	.002	.002

$F = 2$

F (1,13) N.S.

using $Y = MX + b$ (equation for linear regression) mean values of ME intake and liveweight (both expressed in Logs) and a common regression coefficient of 0.922

High (H) $ME = .411LW^{0.922}$

Low (L) $ME = .281LW^{0.922}$

Pooled data $ME = .340LW^{0.922}$