HIGH LEAN CONTENT OR HIGH LEAN GROWTH RATE -IMPLICATIONS FOR NUTRITION

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SUMMARY

The effects of selection for high lean content in the carcass versus selection for high lean growth rates, on parameters such as voluntary food intake, relationship between protein deposition and liveweight, the net efficiency of utilization of apparently digested ideal protein, maintenance energy requirements and changes in the body water:protein ratio were examined. It was concluded that selection for high lean content had been effective in producing animals which attained high lean growth rates at lower energy intakes than those observed where high lean growth rate had been the main basis for selection. Consequently there were marked differences in body composition. Animals selected for high lean content had high maintenance energy requirements which could be "explained" by the higher proportion of lean tissue and possibly by higher rates of protein turnover. They also had higher water: protein ratios in the empty body at slaughter presumably reflecting a younger physiological age. Pigs treated with exogenous growth hormone (GH) showed high rates of lean growth similar to those observed with the The effects on maintenance energy requirements and best selected animals. water:protein ratios were not so marked, presumably due to the limited periods of treatment imposed.

It appeared that the efficiency of utilization of absorbed ideal protein (e_p) was constant for a particular weight range when energy intake was restricted. However, there is clearly an effect of liveweight/age and possibly an effect of genotype which require further research before the (e_p) term can be fully defined. The approach of using a minimum lipid:protein ratio related to genotype is not completely satisfactory and it is probably more scientifically correct to consider lipid deposition purely as the end product of the residual energy available for production after protein gain and maintenance needs have been met, provided that a sufficiently accurate means of predicting e_p can be established. Thereafter the main factor separating different genotypes in terms of growth rates, feed efficiency and body composition is the voluntary food intake.

INTRODUCTION

Genetic selection during the past 30 years has had a dramatic effect on the growth, feed efficiency and body composition of pigs. For example, at the Northern Ireland Pig Testing Station growth rates of gilts improved by 28% and feed conversion ratios by 35% during the period 1970-1992. Eye muscle areas increased by 40% and backfat measurements were halved. Ollivier (1986) reported that an intensive selection programme between 1965 and 1985 resulted in annual increases in lean gain of 6.4 g/d and reductions in feed/lean gain ratios of 0.03.

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From the producer's side of the fence the main aim is to play the system to maintain or improve profit. Because feed costs are such a major component of production improving feed efficiency is the key factor. Since the energy content of lean meat is much lower than that of fat, selection for improved feed efficiency tends to go hand in hand with increased lean growth rates. To some extent therefore, the title of the paper is misleading in that high lean growth rate is a must - not an optional extra. However, it is possible to achieve high lean growth rates and improved feed efficiency but still end up with a reasonably fat carcass if feed intakes are high.

In recent years the increased pre-occupation of consumers with the arguments about dietary fat and health has increased the demand for lean meat in many countries and this has had an impact on selection targets. For example, in the UK, the maximum P2 for top grade pigs in 1983 was 16 mm and today it is 10. However, very high lean contents are frequently associated with low feed intakes and hence not necessarily with the highest rates of lean growth.

The purpose of this paper is to compare the available data on animals of high lean growth potential where selection has been mainly against fat content (as in UK) or for high growth rates (as exemplified in the studies of Campbell and colleagues in Australia). Five specific aspects which are of particular importance to the prediction of nutrient requirements and/or growth will be considered: voluntary food intake, the relationship between liveweight and protein deposition under conditions of adequate nutrition, the efficiency of utilization of absorbed ideal protein, the energy requirement for maintenance and the water:protein ratio in the gain. Where possible comparisons will also be made with pigs treated with growth hormone. In order to simplify discussion only results for boars will be considered.

VOLUNTARY FOOD INTAKE

Growth rates increase up to the highest levels of feed intake achieved. However, it is well known that, with pigs of mediocre genetic potential, lean growth rates reach a plateau at intakes below the appetite limit (Dunkin et al. 1986; Campbell and Taverner 1988).

Two recent studies with improved boars (Campbell and Taverner 1988; Rao and McCracken 1992) demonstrated linear responses in lean growth rate up to the appetite limit and similar maximum rates of lean deposition. Direct comparisons of maximum feed intake are complicated by the different starting weights in the two studies. However, by converting energy intakes on the basis of metabolic body weight (W^{0.63}) it is clear (Fig. 1) that the pigs of Rao and McCracken (1992) attained much lower levels of intake. At similar energy intakes, daily protein gains were about 20% higher than for the strain A pigs of Campbell and Taverner (1988) and 50% higher than for strain B pigs. Consequently, there were marked differences in the lipid/protein ratios in the gain (Fig 2) and the L:P ratio in the whole body of strain A boars at 90 kg was double the value for the Belfast boars. It is difficult to find studies using growth hormone over equivalent weight ranges. The results of Campbell et al. (1989) over the 60-90 kg range have been included in Figs 1 and 2 for comparison. It is satisfying to note that the protein gains of the controls fit perfectly with the strain A pigs of Campbell and Taverner (1988). The GH-treated group did show a reduction in feed intake relative to strain A but still some 10% higher than

those of Rao and McCracken (1992) and the protein gain was above the extrapolated values for the Belfast pigs. The lipid/protein ratio in the gain was similar to that in the pigs of Rao and McCracken (1992) but was higher in the whole body (1.0 vs 0.7), presumably due to a higher fat content at the start of the experimental period.



Figure 1 Relationship between energy intake and protein deposition (□)
McCracken and Rao 1990; (●) Campbell and Taverner 1988 (strain A)
(O) strain B (■) Campbell et al. 1989 (1 control, 2 GH-treated).

RELATIONSHIP BETWEEN PROTEIN DEPOSITION AND LIVEWEIGHT

Whittemore and Fawcett (1976) proposed that, for all practical purposes, a linear/plateau model would describe the relationship between maximum protein deposition and liveweight with the plateau extending between 40-120 kg. This was supported by the results of Whittemore et al. (1988) that rates of protein retention were maintained within 10 g of the maximum over the 45-125 kg range. Rao and McCracken (1991) studied the relationship between protein deposition and energy intake at five stages between 40-90 kg using N balance. The mean values at the two highest levels of energy intake employed (averaging 2.7 MJ DE/W^{0.63}) were 204, 220, 230, 238, 238 g/d for pigs weighing 40, 50, 60, 70 and 80 kg respectively. This suggests that, even at relatively high intakes with pigs of high genetic potential, protein deposition rates plateau between 60-80 kg and contrasts with the result of de Greef (1992) with *ad libitum* fed pigs where protein gains of 159, 198, 221 and 250 g/d were estimated respectively for the weight ranges 25-45, 45-65, 65-85 and 85-105 kg.

In a recent experiment (Urquhart and McCracken 1993) one litter of pigs exhibited unusually high intakes by Northern Ireland standards, more in line with Australian feed intakes. Table 1 summarises the performance of the pig which was fed *ad libitum* and taken to 140 kg. Whilst it is recognised that one swallow does not make a summer the results support the general conclusion that protein deposition rates do plateau between 60-100 kg. They also indicate that it is possible, by natural

selection, to obtain animals capable of at least 250 g/d ie. as high as those observed following GH treatment.

Weight range (kg)	Feed (kg/d)	Gain (kg/d)	Feed:gain	DE intake (MJ/W ^{0.63})	Estimated CP gain (g/d)
40-60	2.59	1.36	1.90	2.92	220
60-80	3.07	1.64	1.87	2.79	270
80-100	3.43	1.59	2.16	2.64	260
100-120	3.70	1.58	2.34	2.52	250
120-140	4.06	. 1.44	2.82	2.50	230

Table 1Performance of boar 8251 fed ad libitum from 40-140 kg

Whittemore (1993) argues that a Gompertz function provides a suitable single expression for the relationship between the potential rate of protein retention ($P\hat{r}$) and body mass. Where $P\hat{r} = B$. Pt ln ($P\hat{t}/Pt$), the potential daily protein deposition ($P\hat{r}$) at any given protein mass (Pt) may be estimated from a knowledge of the rate parameter B and the mature protein mass ($P\hat{t}$). Over the range 40-120 kg body mass the Gompertz equation gives a relatively flat-topped response for Pi:. The above data would fit reasonably comfortably with such a relationship, as did that of Whittemore et al. (1988) although the maximum values would seem to occur at lighter weights than would be predicted by the Gompertz relationship.

NET EFFICIENCY OF PROTEIN UTILISATION

The efficiency of utilisation of absorbed ideal protein is one of the most difficult and important factors in computing protein requirements and has been the subject of much research and debate. Whittemore and Fawcett (1976) proposed a linear-plateau model to describe the interaction between energy intake and protein deposition in the pig and this has been demonstrated in a number of studies. This, coupled with the concept of a minimum lipid/protein ratio in the gain, varying with genotype, has been the basis of most pig growth models. However, it has been clear for a long time that young pigs do not adhere to this concept, being prepared to lose body fat to maintain positive protein balance (eg. McCracken and McAllister 1984). A number of studies on older pigs also demonstrate that the lipid/protein ratio in the gain decreases with restriction of energy intake. This is seen in Fig. 2 from the results of Campbell and Taverner (1988) and was demonstrated in the studies of 'de Greef (1992). In contrast, the net efficiency of utilisation of apparently digested ideal protein (e_p) remains constant when the variable is energy intake (Fig 2) as shown by the results of Campbell and Taverner (1988) and Rao and McCracken (1992). It is notable, however, that the value in both studies is about 0.6. This is in sharp contrast to the statement of Whittemore (1983) that, for all practical purposes,

the value for net efficiency is about 0.85 and is supported by calculations (Table 2) of the probable value for e_p at maximum protein deposition or liveweight gain in a number of studies.



Figure 2 Relationship between energy intake and lipid : protein ratio in the gain of growing boars (\blacksquare) Rao and McCracken 1992 (\bullet) Campbell and Taverner 1988 (strain A) (\blacktriangle , \triangle) Campbell et al. 1989 (control, GH-treated) and calculated values for e_p (\square) Rao and McCracken 1992 (0) Campbell and Taverner 1988.

Table 2Estimates of ep at maximum rate of live weight gain or protein deposition

Source	Weight range (kg)	Calculated e _p
Yen et al. (1986a)	25-55	0.59
Yen et al. (1986b)	50-90	0.62
Giles et al. (1987)	20-50	0.68
Campbell et al. (1988)	8-20	0.60
Campbell et al. (1988)	20-50	0.54
	50-90	0.61
Rao and McCracken (1990)	33-55	0.58
	33-90	0.55

Recently Kyriazakis and Emmans (1992) have proposed that $\mathbf{e_p}$ is linearly related to the energy/protein ratio of the diet under conditions where protein is adequate and energy is limiting and constant at about 0.82 when protein is limiting. This is similar to the observations of Black and Griffiths (1975) with growing lambs except that the latter authors showed conclusively that the slope of the relationship between protein deposition and energy intake decreased with increasing weight of the animals. Fig 1 also demonstrates different slopes of protein deposition and energy intake with different genotypes indicating that the efficiency of protein utilisation is animal driven as well as diet driven. This is further illustrated in Fig 3 where the slope of the relationship between $\mathbf{e_p}$ and the ME:DCP ratio is compared

for the young pigs of Kyriazakis and Emmans (1992) and the older animals of Rao and McCracken (1990) and is also evident in the study of Rao and McCracken (1991) where it was observed that $\mathbf{e}_{\mathbf{p}}$ decreased from 0.69 at 38 kg to 0.51 at 80 kg when the same diet was fed at a series of levels of energy intake (Fig 4.). It is clear from the above discussion that the interpretation of Kyriazakis and Emmans (1992) is too simplistic and that further research is needed to establish an adequate basis for calculating $\mathbf{e}_{\mathbf{p}}$ based on both dietary and animal factors. However, the similarity of the values shown in Table 2 for pigs of different genetic potential, coupled with the recent observation of Kyriazakis and Emmans (1993) that similar relationships exist between $\mathbf{e}_{\mathbf{p}}$ and the ME:DCP ratio for young Landrace and Chinese Meishan pigs, suggest that liveweight/age rather than genetic potential may be the major animal factor. If so, it should be possible to develop an appropriate relationship linking diet and liveweight to be used in combination with P $\hat{\mathbf{r}}$.







Figure 4 Relationship between e_p and liveweight in the study of Rao and McCracken 1991 where the same diet was fed at a series of levels of energy intake ranging from 80 to 160 g per kg W^{0.63} at each of five liveweights.

MAINTENANCE ENERGY REQUIREMENTS

The factorial approach to energy requirements identifies requirements for maintenance, protein deposition and fat deposition and is backed up by a large body of data based on calorimetry and slaughter. The values proposed by ARC (1981) for the maintenance requirement, ME, were 0.458 $W^{0.75}$ or 0.719 $W^{0.63}$. Whittemore (1983) criticised this approach suggesting that the major metabolic processes contributing to the maintenance requirement are associated with the intestines, liver and muscle mass and that an equation of the type $ME_m = 1.85$ Pt 0.78 where Pt is total body protein mass, would be more appropriate since this would increase the maintenance requirement for lean pigs such as entire males. Black et al. (1986) proposed a relationship based on protein mass and growth rate. McCracken and Rao (1989) observed that the "maintenance requirement", ie. residual heat production after correcting for the ARC (1981) costs of fat and protein deposition, was much higher than the predicted ARC (1981) value for maintenance. Similar high values were obtained by Rao and McCracken (1991) using the linear regression approach and it was observed that they were higher than that calculated from the Whittemore (1983) equation but agreed well with the Black et al. (1986) prediction (Table 3). It would therefore appear that the maintenance requirements of boars selected for high rates of lean gain are higher than in unselected pigs thus reducing the energy available for productive purposes.

Table 3Calculated maintenance requirement (MJ/d) for 60 kg pig

ARC (1981)	Whittemore (1983)	Black et al. (1986)	Rao and McCracken (1991)	
9.5	11.3	13.0	13.1	

Interestingly, Campbell and Taverner (1988) reported a large difference in the maintenance requirement of strain A and B pigs. However, recalculation of the data using ARC (1981) costs for protein and fat deposition gives values of 842 vs 775 $W^{0.63}$ which differ by only 8% (not 28% as indicated by regression) and which lie between the ARC (1981) value of 719 $W^{0.63}$ and the value of 982 $W^{0.63}$ determined by Rao and McCracken (1991).

The effect of growth hormone on maintenance requirements is still open to debate. Although Campbell et al. (1988) and Campbell et al. (1991) reported increases of 17 and 28% respectively for GH-treated pigs by linear regression, recalculation of the "residual heat production" using ARC (1981) costs for protein and fat deposition gives identical mean values (10.9 MJ) for the controls and GH-pigs in the first study. Similar calculations also show no effect of GH on "maintenance" in the study of Campbell et al. (1989). However, in the experiment on the effects of dietary protein (Campbell et al. 1990) the mean residual heat production of GH-treated pigs was 23% higher than for controls.

BODY WATER: PROTEIN RATIO

Water is by far the largest component of body mass. In modelling pig growth and nutrient requirements it is normally predicted by an equation relating to body protein mass (Pt). The water:protein ratio declines sharply with increasing weight and Kotarbinska (1969) obtained the relationship:

Water mass = $4.9 \text{ Pt}^{0.855}$

Stranks et al. (1988) predicted that the water:protein ratio would change with genetic potential for lean deposition and proposed the relationship W = 4.85 Pt^{0.89} for pigs of high genetic potential. The results of Campbell and Taverner (1988) indicated that the ratio was higher at 90 kg in strain A boars compared with strain B (3.40 vs 3.12). However, the values observed by Rao and McCracken (1990; 1992) are 10% higher than those for strain A boars, 15% higher than predicted by the Kotarbinska (1969) equation and 20% higher than the strain B boars or those of Whittemore et al. (1988). De Greef (1992) studied the relationship over the range 4-18 kg and obtained the equation W = 5.4 Pt^{0.855}. This equation agrees quite well with the high values observed in Northern Ireland but tends to underestimate, particularly at high weights. McCracken et al. (1991) studied a range of Pt from 6-52 kg and the relationship which best fits the rather limited data is W = 5.3 Pt^{0.87}.

These higher values for the water:protein ratio at 90 kg in improved pigs are consistent with the expectation of higher mature weight and protein mass and hence a younger physiological age at 90 kg. This view is confirmed by the results of McCracken et al. (1991) who predicted a mature protein mass of 55 kg compared with the earlier estimates of 38 kg for the unimproved pigs of Whittemore et al. (1988). What then of pigs treated with GH? It would seem that they are not significantly different from controls despite the large shifts in lipid/protein ratios. For example the mean values for control and GH-treated were respectively 3.76 and 3.80 (Campbell et al. 1988), 3.38 and 3.43 (Campbell et al. 1989), 3.43, and 3.47 (Campbell et al. 1990). It can perhaps be concluded that exogenous GH does not alter mature body mass but the rate at which this is attained. On the other hand it may be that the periods of GH administration have been too short to demonstrate the effect on mature weight. To the author's knowledge these hypotheses have not yet been tested to their ultimate conclusion.

CONCLUSIONS

The high rates of protein gain shown by animals selected for high lean content and feed efficiency, coupled with the tendency for animals treated with growth hormone to show reduced feed intakes and increased rates of lean deposition, suggest that a reduction in voluntary food intake may be an inevitable consequence of selection for high lean growth rate and improved feed efficiency. The associated increase in 'maintenance requirement' gives rise to a reduction in productive energy and hence to a reduction in gross energetic efficiency: However the increased rate of protein deposition in combination with higher water:protein ratios gives rise to the paradox of reduced energetic efficiency but improved feed conversion efficiency.

The results reviewed suggest that changes in genetic potential for protein deposition do not, per se, alter the net efficiency of utilisation of absorbed protein. Further, there is good evidence that e_p is unchanged as the feeding level of a particular diet is reduced. Since it is clear that the concept of a minimum lipid:protein ratio is not strictly correct, it would be preferable to predict the response of protein gain to changes in feed intake through e_p provided that an acceptable means of calculating e_p could be determined. This would permit the calculation of lipid retention as the end product of meeting the energy needs for maintenance and protein deposition. The results in Table 2 suggest that e_p is about 0.6 for maximum rates of protein deposition in pigs between 40-90 kg whereas it is possible that values of up to 0.8 may apply with younger pigs (Kyriazakis and Emmans 1992). Although in the study of McCracken and Rao (1990) protein deposition increased linearly and the lipid:protein ratio in the gain fell linearly to the highest level of protein employed it is likely that such levels of protein would not always provide the best economic return. Until a more scientific approach can be devised it is suggested that a value for e_p of about 0.7 would be a reasonable compromise for pigs above 30 kg.

Having calculated crude protein requirements on a daily basis it is easy to convert them to dietary concentration provided that sound information is available about the expected level of feed intake. In this respect three points need to be borne in mind. Firstly, feed intakes of group-housed pigs fed *ad libitum* are generally lower (up to 15%) than those fed individually as was the case in the experiment discussed above. Secondly, there is a wide range of individual intakes within a herd and even within litters (McCracken and Stockdale 1989) and any formulation must necessarily be something of a compromise. Thirdly, the required dietary crude protein concentration falls rapidly with increasing liveweight and unless a sophisticated system for adjusting the crude protein content can be applied, any diet will be a compromise probably undersupplying protein at the start of the feeding period and oversupplying at the end.

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