

Selection for leanness and the energetic efficiency of growth in meat animals

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When selecting animals for meat production it is commonsense to favour those individuals that grow to the right size and the right body composition in the shortest possible time and at the least cost in terms of animal feed. In practice, selection of animals is usually based on some index that combines performance in different traits to produce a single value for the comparison of genetic worth (see Fowler, Bichard & Pease, 1976). To review the effects of different selection procedures on the efficiency of growth and to analyse the biological reasons for these effects would be to review a major part of the science both of animal breeding and animal physiology. This paper is intended only to show how the calorimetric approach can be used to examine the partition of food energy between protein deposition, fat deposition and heat loss in a number of laboratory animals and meat animals known to differ markedly in body composition, and to relate this to differences in the efficiency of utilization of food energy for growth.

Growth is a confusing process to evaluate because everything is changing at once. However, there are certain absolute principles that apply to all animals allowed to grow without interruption or environmental constraint and given good quality food in adequate amounts or *ad lib.* In these ideal circumstances, animals increase in body-weight (W) along a sigmoid curve until they reach a mature body size (A) although they may continue to deposit fat thereafter. Relative growth rate ($\frac{dW}{dt} \div \frac{1}{W}$) declines throughout from birth to maturity (Brody, 1945). The proportion of fat relative to protein deposited in the growing animal increases progressively as the animal proceeds to maturity. The amount of food energy required to maintain energy balance increases throughout growth as does the ratio of maintenance requirement to *ad lib.* intake (Blaxter, 1968). All these factors combine to reduce throughout growth the net efficiency with which food is converted into body tissue and reduce even more the efficiency with which it is converted to protein or lean meat. Thus, other things being equal, the animal that is farthest from its mature size (A) will have the greatest relative weight gain, the leanest carcass and the most efficient conversion of food to lean body tissue. It follows that selection for any or all of these traits to a fixed body-weight will inevitably favour the animal that is physiologically less mature and thus select for an increase in A (Taylor, 1968).

Whether a farmer should raise large or small animals is an important question, but it is no more a genetic question than would be one as to whether he should

raise pigs or chickens. Moreover, selection for absolute growth rate has not had an appreciable effect on relative growth rate (which would be of genetic merit for meat animals) in mice (Roberts, 1961; Timon & Eisen, 1969) or cattle (Taylor, 1970). Direct selection for relative growth rate at a fixed value for W also tends to increase A since it is proportional to $(A-W)$ (Bakker, 1974).

At the Rowett Institute we have been comparing energy utilization during growth in animals that differ markedly in body composition in a way that is not obviously related to differences in A . The model used to describe energy flow is shown in Fig. 1. Metabolizable energy (ME) is food energy minus the sum of all the combustible materials in the excreta and serves as the physiological fuel for the body. Nearly all energy is stored as protein or as fat. The energy value of protein is 23.7 MJ/kg, but each kg of tissue protein (except hair and wool) is associated with 3.5 to 4.0 times its weight of water so that the energy retained in 1 kg of fat-free muscle tissue is only about 5 MJ. Fat, by contrast, contains 39.3 MJ/kg so that the same amount of ME is deposited in 1 kg of fat as in about 8 kg of fat-free muscle.

The ME not retained as protein or fat is lost as heat (H). Kielanowski (1976) proposed that this large component of ME flow (seldom less than 70%) be analysed statistically into that related to protein deposition, fat deposition and 'maintenance', a residual term relating H to W . In reviewing experiments conducted during normal growth with rats and pigs, Kielanowski concluded that, in simple-stomached animals getting a high quality, high-carbohydrate diet, the increments in H associated with the deposition of 1 kg (24 MJ) protein and 1 kg (39 MJ) fat were about 31 and 16 MJ, respectively. In other, more convenient words, the ME required to deposit 1 kg of protein or fat is the same, about 55 MJ, although the deposition of 1 kg protein is associated with about twice as great an increment of H (31 MJ) as the deposition of 1 kg fat (16 MJ) (Fig. 1). In all the experiments reviewed by Kielanowski certain more or less valid assumptions were made as to the large residual or 'maintenance' component of H and its relation to W .

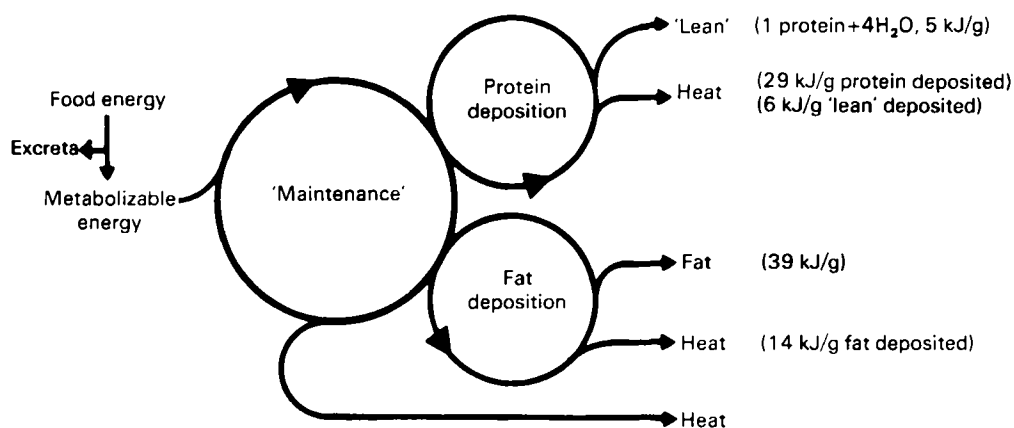


Fig. 1. Pathways of food energy utilization by growing animals (for further explanation see above).

Our first attempt to see how the energetic efficiency of growth was affected by the partition of retained energy between protein and fat made use of the Zucker rat in which obesity appears as a recessive gene (Zucker & Zucker, 1961). Congenitally obese (fatty) individuals eat more than their lean siblings if they get the chance. However, when the two phenotypes are pair-fed, the proportion of energy retained as fat is still much higher in the fatty rats and protein deposition is stunted. In fact, food intake appears to be regulated in both phenotypes so as to sustain a normal, comparable rate of protein deposition (Pullar & Webster, 1974; Radcliffe & Webster, 1976).

Pullar & Webster (1976) have compared the flow of ME to protein, fat and heat in fatty and lean Zucker rats in a way that makes no a priori assumption as to the maintenance component of H. The values obtained were 53 kJ ME/g protein or fat deposited, reassuringly close to those preferred by Kielanowski (1976). However, even when the energy costs of deposition have been taken into account it still takes about five times as much ME to deposit a gram of fat as a gram of wet tissue protein (Fig. 1). Very little information is available on the energy costs of simultaneous protein and fat deposition in ruminant animals (see Kielanowski, 1976), but relative efficiencies of the two processes may be about the same (Ørskov & McDonald, 1970).

The residual maintenance component of H is traditionally assumed to be the same function of body-weight (or W^n) for different phenotypes within the same breed or species, or even for different species (Kleiber, 1961). On this assumption one could predict exactly how much more efficient the lean animal would be at converting the same ME intake into body gains. There is, however, a body of evidence, growing rapidly in recent years, which indicates that in growing animals 'maintenance' H is not a constant function of W^n (see for example Frisch & Vercoe, 1976; Keller & Piekarczywska, 1976; Kielanowski, 1976; van der Wal, Versteegen & van der Hel, 1976; Webster, Smith & Mollison, 1976). In some cases differences in H may be linked directly to differences in activity (Wenk & van Es, 1976), but in others it appears that selection for leanness could have been achieved simply by manipulating the partition of ME between heat and fat without achieving any net gain in the efficiency of lean meat deposition.

Table 1 compares some of the commonly measured growth traits in lean and fatty Zucker rats pair-fed and offered food *ad lib*. The values are taken from Radcliffe & Webster (1976). The proportion of energy retained as protein and as fat, respectively, was about 0.3 and 0.7 in lean and 0.1 and 0.9 in fatty rats whether pair-fed or allowed food *ad lib*. The lean rats converted food to protein gain 50% more efficiently than the fatty rats, but also dissipated a far higher proportion of ME as heat. Consequently, although the energy deposited per g of weight gain was much higher in the fatty than the lean rats, they still put on weight faster than the lean rats at the same food intake, and thus had a higher efficiency of food conversion to body-weight gain. This extreme example of an effect of phenotypic differences in body composition on the energetic efficiency of growth is included to show that some of the correlations usually observed in

selection experiments, such as that between leanness and food conversion efficiency in pair-fed animals, do not always occur.

Table 1. Cumulative values for energy exchange, weight gain and feed conversion from 32 to 66 d of age in lean and fatty Zucker rats, fed ad lib. and fatty rats pair-fed to the ad lib. intake of their lean siblings. The diet contained 20.2 kJ metabolizable energy (ME)/g dry matter (DM) and 443 g/kg crude protein

	Pair-fed			Ad lib.	
	Lean	Fatty	Lean:fatty	Fatty	Lean:fatty
ME intake (MJ)	8.50	8.80	—	13.90	0.61
Energy gain as protein (MJ)	0.59	0.41	1.44	0.63	N.S.*
Energy gain as fat (MJ)	1.47	3.39	0.43	5.82	0.25
Heat loss (MJ)	6.44	5.00	1.29	7.45	0.86
Protein gain/ME intake (kJ/MJ)	69	46	1.50	45	1.53
Weight gain (g/d)	4.3	5.4	0.80	8.2	0.52
Food conversion efficiency (g gain/g DM)	0.33	0.40	0.82	0.38	0.87

*N.S., no significant difference.

The Pietrain pig has been selected for leanness. Lister (1976) claimed that the Pietrain appeared to be no more efficient than the fatter Large White pig at converting food into lean tissue gain and suggested that selection may have been for an increase in metabolic heat production, which would not only restrict fat deposition but also increase susceptibility to environmental stressors. Fuller, Webster, MacPherson & Smith (1976) have compared ME flow to protein, fat and heat in Pietrain and Large White×Landrace pigs. When pair-fed there was absolutely no suggestion of differences between the two breeds in heat production or the chemical composition of the body gains although the Pietrains obviously differed in shape from Large White×Landrace pigs. The Pietrains had significantly lower appetites when offered food *ad lib.* It is, of course, quite possible that the small number of Pietrain pigs we used were of a markedly different strain from those used by Lister, but we were forced to conclude that the only explanation for the comparative leanness of our Pietrains was a low appetite.

Another animal which has been advocated as being lean and therefore efficient is the red deer (Blaxter, 1975). In a PhD research programme conducted at the Rowett Institute, Simpson (1976) compared red deer and lambs given the same amounts of the same diet at about the same stage of growth. There are some difficulties in interpreting this study because of differences between the species in mature weight, and also because protein deposition was estimated from nitrogen balance studies which did not give reliable estimates of tissue protein gains (see Duncan, 1966). Nevertheless there was no difference between the species in the apparent retention of dietary N. Estimated heat production at maintenance was about 500 and 340 kJ/kg $W^{0.75}$ per 24 h for red deer and sheep, respectively. The small number of experiments done with red deer at the Rowett Institute point to

essentially the same conclusions as those reached by Holter, Hayes & Wiley (1976) from much more extensive studies with the white-tailed deer. In essence the reduced fatness of the deer compared with the sheep appears to be associated with an equivalent increase in ME lost as heat. This confers no energetic advantage to the growing animal. Moreover, increased energy requirement for maintenance of the adult is a considerable disadvantage particularly in the case of the red deer hind producing only one offspring per year.

The energetic efficiency of growth in beef cattle is our major concern. Although these experiments proceed at a rather stately pace, dictated by the growth patterns of the animals themselves, some firm conclusions are possible at this stage. Table 2 compares estimates of the cumulative flow of ME to protein, heat and fat in Hereford×Friesian bulls and steers pair-fed from 100 to 430 kg live weight. Energy balance was estimated from calorimetric experiments, protein and water retention from $^2\text{H}_2\text{O}$ space (Webster, Crabtree, Smith & Mollison, 1976; Webster, Smith & Mollison, 1977). Bulls took 36 d less than steers to reach 430 kg so that although they were pair-fed on a body-weight basis they actually consumed 9% less ME. The proportion of energy retained as protein was 14% greater in the bulls and the proportion of fat 23% less. This is because the daily heat production of the bulls was nearly 10% greater than steers at the same W and ME intake. Despite this the total loss of ME as heat was lower in the bulls because they took less time to get to 430 kg. Differences between bulls and steers in weight gain and food conversion efficiency were similar to those reported by Preson, MacDearmid, Aitken, McLeod & Philip (1968) and by Kay, Kilkenny, Sutherland, Swan & Tallack (1974).

Table 2. *Cumulative values for energy exchange, weight gain and food conversion in Hereford×Friesian bulls and steers pair-fed a diet containing 12.2 MJ metabolizable energy (ME)/kg dry matter (DM) from 100 to 430 kg live weight*

	Bulls	Steers	Bulls:steers
Duration (d)	254	290	0.88
ME intake ($\text{MJ} \times 10^3$)	17.54	19.35	0.91
Energy gain as protein ($\text{MJ} \times 10^3$)	1.16	1.02	1.14
Energy gain as fat ($\text{MJ} \times 10^3$)	3.24	4.22	0.77
Heat loss ($\text{MJ} \times 10^3$)	13.14	14.11	0.93
Protein gain/ME intake (kJ/MJ)	66	53	1.24
Weight gain (kg/d)	1.30	1.14	1.14
Food conversion efficiency (kg gain/kg DM)	0.23	0.21	1.09

The greater leanness of the bull than the steer is therefore associated with a significant increase in the daily loss of ME as heat, but in this case, this loss is more than balanced by a greater efficiency of lean meat deposition and a much lower energy content of total empty body-weight gain.

A complete comparison cannot yet be made between steers of different breeds. Nevertheless we have observed that Friesian steers produce significantly more heat (about 15%) than Hereford×Friesians at the same W and ME intake. This

difference is apparent within a week of birth (Webster & Gordon, 1977) and persists to a body-weight of 500 kg (Webster, Smith & Mollison, 1977). Undoubtedly the Friesians tend to be leaner than the Hereford×Friesian, but whether there are differences between the breeds in the efficiency of protein deposition we do not yet know. Certainly the higher heat production of the Friesian breed suggests that a Friesian cow will have a higher energy requirement for maintenance than a Hereford×Friesian of comparable weight.

The only general conclusion that can be drawn from this survey of energy balance trials with growing animals is that no general conclusions relating leanness to the efficiency of growth in meat animals are possible. Examples have been presented of leanness being associated with reduced food conversion to body-weight but increased efficiency of protein deposition (the Zucker rat), reduced appetite (the Pietrain pig), increased heat production (the red deer) or improved food conversion despite increased heat production (the Hereford×Friesian bull). The trouble with calorimetric experiments is that they are expensive and time-consuming and therefore only suitable for studies involving small numbers of animals. For most farm animals, however, they are cheaper and quicker than experiments involving comparative slaughter and carcass analysis. In future, the calorimetric approach could be used to obtain a detailed picture of energy flow in individuals from two lines of animals after they had been selected for an appropriate number of generations for the more easily measured traits usually recorded in genetic experiments relating to growth.

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