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SYMPOSIUM ON
'COMPARATIVE ASPECTS OF BODY COMPOSITION OF FARM AND LABORATORY ANIMALS'

Factors affecting the body composition of growing and adult animals

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The body composition of any animal is the consequence of the effect of nutrition over a period of time on the genetic and physiological factors that, together with nutrition, determine its phenotype. This paper will consider only those aspects of body composition that are of major importance, first in the conversion of animal feed to saleable product in meat animals and, secondly, in the quality of the meat as perceived by the consumer. These are (a) killing-out ratio, i.e. empty carcass weight:total body-weight at the time of slaughter; (b) the proportions of dissectable bone, lean and fat in the carcass; (c) the chemical composition of the lean and adipose tissue.

The quantity of published information on the body composition of meat animals (and laboratory species used as models for meat animals) is enormous. This paper deals mainly with beef cattle. The Agriculture and Food Research Council (Agricultural Research Council, 1980) has produced a very comprehensive review of the literature relating to the body composition of ruminants. This brief paper is not intended to compete with this review nor does it attempt to bring it up to date in a bibliographic sense. Its purpose is only to outline the range of genetic, physiological and nutritional factors that affect body composition and explore the interactions between them.

Let us suppose it was possible to make a precise estimate, in vivo, of the body composition of all Charolais and Hereford pedigree bulls reared on their farms of birth to 400 d. Meat and Livestock Commission figures (Allen & Kilkenny, 1980) indicate that the weights of Hereford and Charolais bulls range between 319–591 and 436–779 kg respectively. Clearly some of the difference between bulls in weight-for-age has been genetic, some environmental. Representative equations given by the Agricultural Research Council (1980, Tables 1.21 and 1.22) to predict the fat content of the empty carcass after correction for breed and rate of gain/d,

estimate fat contents for the smallest Hereford and largest Charolais bull to be approximately 140 and 260 g/kg respectively. In other words, the largest Charolais is predicted to be 85% fatter than the smallest Hereford at 400 d of age! This rather extreme example and its highly improbable solution illustrate three important points. First, comparisons between animals within a species or even within a breed at a constant weight or age in terms of body composition or the efficiency of food conversion during growth are dominated by the effect of stage of maturity. The individual having the larger mature size will, by definition, be less mature at a given weight or age (Taylor, 1965) and thus (other things being equal) tend to be leaner. In this example, one would rarely expect to find a healthy, properly-fed Hereford bull to be leaner than a Charolais bull at 400 d. Second, the mean values and correction factors given by the Agricultural Research Council (1980) cannot be used with confidence to predict either the composition of gains in a particular phenotype fed on a particular ration or the age and weight at which its body composition will be ideal for slaughter. The third, and perhaps most important point is that many experiments which attempt to interpret information on body composition in terms of relatively few variables such as breed, sex and plane of nutrition are impossible to interpret because they fail to take other vital factors into account, the most important of which is undoubtedly stage of maturity. However, so long as one recognizes *a priori* that every factor affecting body composition interacts with every other, it is possible to make certain cautious statements about each individual contributor.

Genetic factors

The most obvious difference between different genotypes is in mature size. The Charolais breed is, on average, larger than the Hereford breed although, as indicated already, the variation between individuals within each breed is far greater than that between mean values for the two breeds (425 and 553 kg at 400 d; Allen & Kilkenny, 1980). The Hereford is commonly referred to as an 'early-maturing' breed relative to the Charolais. In fact when growth rates of both breeds are scaled according to mature size$^{0.25}$ to create the concept of 'metabolic time' (Kirkwood & Webster, 1984), both Hereford and Charolais bulls mature at about the same rate, faster than both Friesian and Aberdeen Angus (Webster *et al.* 1982). Hereford and Aberdeen Angus bulls, fed close to *ad lib*, probably reach 20% fat in the carcass (i.e. 'finish') at a lower weight relative to mature size than Charolais bulls. In other words, the Hereford is (relatively) early maturing and early fattening, the Charolais early maturing but late fattening and the Aberdeen Angus late maturing but early fattening. This is, however, a difficult concept to incorporate into a growth trial since it can only be deduced retrospectively from a knowledge of mature size.

Recent publications from the Meat and Livestock Commission (e.g. Kempster *et al.* 1982; Southgate, 1982) have overcome part of the problem by comparing animals at constant 'finish' using the Scanogram ultrasonic machine. This is an obvious improvement on comparisons at fixed weight or age and while it cannot

Table 1.   *Genetic effects on body composition at constant 'finish' (from Southgate,*
1982)

Sire breed ...	Angus	Charolais	Hereford	Limousin
Wt at slaughter (kg)	393	494	410	454
Feed conversion ratio (g gain/kg feed)	86[a]	82[a]	88[a]	85[a]
Killing-out (%)	52·5[a]	54·8[b]	52·3[a]	54·7[b]
Saleable meat in carcass (%)	72·5[bc]	72·7[b]	71·9[c]	73·3[a]
Saleable meat in expensive cuts (%)	44·1[c]	44·8[b]	44·1[c]	45·4[a]
Fat trim in carcass (%)	9·6[b]	9·0[a]	9·7[b]	9·2[a]

[a,b,c] Values with the same superscript letter did not differ significantly.

discriminate between early fattening and early maturing, which is of importance to the cattle feeder, it does evaluate the animals at the point where their composition is deemed right for the consumer.

Table 1 (from Southgate, 1982) compares aspects of carcass composition for the offspring of different sire breeds and Hereford × Friesian or 'Blue-Grey' cows. Differences were quite small but animals sired by Charolais and Limousin bulls did yield more saleable meat and had less fat trim than the offspring of the British bulls, differences which were both statistically and commercially significant. Although non-genetic influences cannot be ruled out altogether, these observations confirm the popular and visual impression that there are fundamental differences in shape and composition between genotypes. Truscott *et al.* (1983) compared body composition and fat distribution in Hereford and Friesian steers fed *ad lib.* and slaughtered at different stages of growth. By 20 months of age Herefords had only 8% more dissectable fat in the carcass than Friesians. The major difference between the breeds was in the partition of fat. Herefords deposited much more dissectable fat subcutaneously whereas Friesians deposited more in the intra-abdominal regions. Intermuscular fat content (the portion that gets eaten) was about the same for the two breeds. These differences are typical of those which exist between beef and dairy breeds. A predisposition to lay down fat subcutaneously is an obvious consequence of traditional selection in beef breeds. Increased intra-abdominal fat in dairy breeds probably results from selection for milk yield since fat from this depot has a relatively greater blood supply and can be mobilized very rapidly.

The most dramatic effect of genotype on body composition is seen in the case of hereditary muscle hypertrophy (culard or 'double muscling'). The extent of hypertrophy is about 25–30% in muscles of both the anterior and posterior limbs (Hanset & Ansay, 1972) and the overall effect is to create a large increase in killing-out ratio. Table 2 compares double-muscled Aberdeen Angus bulls with normal bulls and F_1 hybrids (Theissen & Rollins, 1982). The homozygous individual is not particularly fast growing and carries a number of undesirable traits (Menissier, 1982) but its F_1 hybrid offspring do appear to grow normally and carry some commercial advantage in terms of carcass composition (Table 2).

Table 2. *Body composition of Aberdeen Angus bulls with and without muscle hypertrophy and in F_1 hybrids (from Theissen & Rollins, 1982)*

	Hypertrophied bulls (H)	Normal bulls (N)	F_1 bulls (H×N)
Wt at slaughter (kg)	488	490	492
Age at slaughter (d)	521	480	468
Killing-out (%)	69·8	62·6	64·3
Adjusted rib-eye area (mm²)	380	250	270
Subcutaneous fat thickness (mm)	4·5	9·9	8·6

Physiological factors

The major physiological influences that interact with nutrition to determine body composition are primarily mediated by hormones. The rate of release of these hormones may be (1) a natural consequence of the sex of the animal and its degree of maturity, (2) modified by manipulation of the external environment (e.g. photoperiod) or (3) modified by manipulation of the internal environment via exogenous hormones or immunological techniques.

Sex and sex hormones. As a general rule, intact males tend to be leaner than castrate males or females. Treatment of castrates and females with exogenous hormones is designed mainly to achieve the growth and carcass characteristics of the intact male. The commercial success of anabolic steroids is well documented but the interpretation of their effects is not always clear. Fisher *et al.* (1985) have recently reported the results of comparisons between twin cattle mostly of the Friesian breed. Some of these are summarized in Table 3. In this trial, bulls did not eat significantly more than steers but did grow faster. They contained less

Table 3. *Growth and carcass composition in twin cattle at 400 d (from Fisher et al. 1985)*

	Steer (S1)	Bull (B1)	S1/B1	Implanted steer (S2)	Bull (B2)	S2/B2
Food intake (kg; 90–400 d)	2339	2459	NS	2638	2614	NS
Food conversion ratio (kg feed intake/kg wt gain)	8·3	7·9	NS	8·4	8·1	NS
Empty body-wt (kg)	327	354	0·93*	368	371	NS
Carcass composition (g/kg side wt)						
Lean	601	657	0·91**	604	654	0·92**
Subcutaneous fat	94	60	1·55**	96	65	1·48**
Intermuscular fat	144	117	1·22**	145	122	1·19**
Chemical composition of lean (mg/g)						
Water	734	742	NS	745	746	NS
Protein	207	217	0·95**	204	209	NS
Lipid	42·5	24·8	1·71*	36·8	27·7	1·33**

NS, not significant.
*$P<0·05$, **$P<0·01$.

subcutaneous fat (which can be easily trimmed) and intermuscular fat (which cannot). This was reflected in the chemical composition of the lean. Implanting steers with trenbolone acetate and oestradiol-17β made their growth rate comparable to that of bulls but, rather surprisingly, their carcass composition was still essentially that of a steer.

The external environment. Severely-cold conditions not only reduce growth rate by increasing energy losses as heat, they may also have profound effects on all aspects of body composition. Dauncey & Ingram (1983) compared young piglets kept at 10° or 35° and showed that those kept cold had relatively shorter limbs, ears and snouts; those raised in the warm retained a greater proportion of protein in muscle. Fat differences were due mainly to differences in energy retention. These effects may be attributed in part to differences in blood flow to superficial tissues and the extremities and in part to endocrine consequences of adaptation to cold (Macari *et al.* 1983). Photoperiod affects growth rate in sheep and, to a lesser extent in cattle, the effect being mediated at least in part by prolactin (Schanbacher & Crouse, 1980). It is probable that long days increase prolactin secretion and this increases the ratio, protein:fat deposition. In natural daylight, prolactin levels decrease sharply at the beginning of autumn (Schams, 1972) and sheep and cattle then shift the partition of retained nutrients from further lean tissue growth towards fat deposition. The evolutionary advantage of this should be obvious to any biologist. The economic disadvantage has been apparent for many years to commercial producers of fat lambs.

Effects of maturity. Given a sufficiency of all nutrients and no major environmental constraints, animals proceed towards their mature size along a sigmoid curve for cumulative growth. Relative rates of growth of individual tissues, organs or muscles are conventionally described by the allometric equation $Y = aX^b$ (Huxley, 1932). Bone, for example is an early-maturing tissue ($b<1\cdot0$), fat is late maturing ($b>1\cdot0$). Changes with maturity in the composition of the body, whether described by simple criteria, such as muscle:bone, or more complete accounts of individual muscles and the distribution of fat depots, can be conveniently described by allometric or similar equations (e.g. Butterfield *et al.* 1983). However, these growth equations are no more than convenient exercises in curve fitting, which describe observed changes during growth with reasonable precision. It is a mistake to assume that relative growth of different tissues is governed by an allometric law. In practice, relative growth of (say) muscle and fat appears to change rather more abruptly with, for example, puberty. Moreover, the *b* values obtained for different tissues do not resolve themselves to unity as they should (see Parks, 1982). The fact remains that stage of maturity (probably best defined as a proportion of mature lean mass) is the major non-nutritive determinant of the composition of the body and predictor of the composition of subsequent body gains. Unless stage of maturity is known, and this requires knowledge or accurate prediction of mature mass, then attempts to interpret differences in body condition to genotype, nutrition or physiological state have little meaning.

Nutritional factors

It should be obvious that the body composition of any animal at any age, weight or stage of maturity can be influenced to a very great degree by both the quantity and quality of food that it has received. Restricting food intake during growth not only reduces rate of body-weight gain but reduces the ratio, fat:protein deposition so that at any given weight, age or proportion of lean body mass the restricted animal will contain less fat relative to lean. The practical implication of this is that one can manipulate the ratio, lean:fat (although not conformation) in the carcass of any genotype to a greater degree than that which exists between the means of different genotypes of commercial importance. Reducing fat content by nutritional means has usually, although not inevitably, implied reduced intake and so a reduction in growth rate. Selection and feeding for extreme leanness in pigs has also created problems in the perceived quality of the adipose tissue, due in part to an increased content of water and in part to an increased concentration of unsaturated fatty acids (especially linoleic). This important topic is outside the scope of this paper but has been excellently reviewed by Wood (1981).

It is possible, by varying the quality of the diet, to vary the body composition of animals permitted to eat *ad lib.* and grow at their own rate. This approach which has important implications for feeding strategies for meat animals implies, in my opinion, that animals have certain targets for growth and body composition and they vary their intake of different diets in order to achieve them as best they can. An alternative school of thought, represented by Blaxter (1968) and Parks (1982) argues on mathematical grounds that growth rate and body composition in animals are simply consequences of the amount of nutrients they consume and of course this is so. However, this begs the question as to whether the animal recognizes its own body composition and regulates its intake of nutrients accordingly. Adult humans, possessing a sense of self-awareness, make conscious decisions as to the importance they attach to their body composition but I suggest that there is more than this to appetite control. Consider two adults, one who manages to gain only 5 kg body-weight between the ages of 20 and 40 years. Such an individual will have balanced metabolizable energy (ME) with heat loss with a precision better than 1:1000. The second adult has apparently attached little importance to his body composition and increased weight from 80 to 120 kg (about 6 stone) over 20 years. In this example, ME intake has, in fact, only exceeded energy expenditure by 1·3%. In the absence of any convincing evidence for regulatory dietary-induced thermogenesis in the adult human (Girardier & Stock, 1983) this suggests a precise control of food intake in even the most extreme cases.

Radcliffe & Webster (1978, 1979) investigated growth and body composition in congenitally obese and lean Zucker rats offered *ad lib.* during growth a wide range of diets varying in protein concentration and quality, carbohydrate quality and proportion of ME in the form of fat. Table 4 presents measurements made of protein and fat retention between 34 and 66 d in rats given diets that did not impair the normal rate of lean tissue growth for any sex or phenotype. These

Table 4. *Gains (g) of protein and fat from 34 to 66 d in lean and 'fatty' Zucker rats offered different diets ad lib.* (from Radcliffe & Webster, 1978, 1979)

Dietary variants (g/kg)	♂				♀			
	Lean		Fatty		Lean		Fatty	
	Protein	Fat	Protein	Fat	Protein	Fat	Protein	Fat
300 Casein + 20 fat	—	—	—	—	25·1	29·4	23·9	135
700 Casein + 20 fat	—	—	—	—	24·3	20·1	24·3	78
300 Gluten + 20 fat	—	—	—	—	26·0	28·4	23·8	134
700 Gluten + 20 fat	—	—	—	—	26·0	18·9	23·5	85
300 Casein + 200 fat	40·6	61·6	31·3	202	26·8	34·2	24·9	178
700 Casein + 200 fat	41·2	39·9	32·1	94	25·4	26·8	25·1	135
300 Casein + 150 cellulose + 20 fat	40·2	37·0	29·8	169	26·2	23·2	26·2	153
300 Casein + 300 cellulose + 20 fat	36·0	23·2	31·3	141	25·6	22·0	25·3	128
Coefficient of variation (%)	6·0	39·3	3·1	30·2	3·0	20·6	3·7	26·7

results may be summarized as follows: (1) food intake was precisely regulated in each sex and phenotype so as to sustain a constant, maximum rate of protein deposition which may be interpreted as being the target for that phenotype. Coefficients of variation for protein deposition were small and relatively constant for male and female lean and fatty rats; (2) rates of lipid deposition (and weight gain) varied enormously in all phenotypes in a way that reflected the ratio, ME: metabolizable protein in the diet; i.e. fat deposition was increased by increasing dietary fat from 20 to 200 mg/g, and reduced by increasing dietary cellulose from 0 to 300 mg/g. Moreover, the coefficient of variation in fat content was similar for lean and fatty rats, which adds weight to the suggestion that the control of food intake, and the consequences thereof for body composition, were normal for rats as a species and not some aberration of the congenitally obese mutant. The most important conclusion to be drawn from this study is that in rats (at least) there is a target for lean tissue growth which dominates the control of food intake. During this time the animal pays little, if any, attention to body fat content so that it is possible, by manipulation of the quality of the diet to (1) sustain maximum lean tissue growth and (2) manipulate carcass composition over a very wide range.

In meat animals, the objective is to achieve maximum lean tissue growth rate while (1) minimizing feed costs and (2) avoiding excess carcass fat. The consumer is putting great pressure on the producer to achieve the latter objective. The producer who responds by reducing the ration of his animals so as to slow down both protein and fat deposition in a particular phenotype is penalizing himself. As far as he is concerned, the most profitable ration is the one that generates lean tissue growth at least cost, whatever the accompanying fat content. The values in Table 4 suggest that fat content can be manipulated through dietary control without incurring the penalty of reduced lean tissue growth rate. Some of these dietary variations may not, however, be cost effective. In that event the meat industry has recourse to the most effective way of manipulating the fat content of the carcass; they can cut it off.

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