MANIPULATION OF BODY COMPOSITION THROUGH NUTRITION

J.L. BLACK*

I. INTRODUCTION

The influence of nutrition on the body composition of animals has been reviewed on numerous occasions recently (Elsley, McDonald and Fowler 1964; Tulloh 1964; Fowler 1968; Reid et al. 1968; Lodge 1969; Allden 1970; Lohman 1971; Young and Sharma 1973). It is now generally agreed that although both plane of nutrition and chemical composition of the diet can have a major effect on body composition when comparisons are made between animals of the same age, these differences are substantially reduced when comparisons are made at the same body weight. Nevertheless, within this general concept, there are opposing viewpoints. Tulloh (1964) and Reid et al. (1968) hold that, for animals of the same breed and sex, body composition is determined by body weight and is virtually independent of nutritional history. On the other hand, Elsley et al. (1964), Fowler (1968) and Lohman (1971) contend that although the proportions of muscle and bone, or protein, water and ash, have a constant relationship to the weight of the fat-free body, the amount of fat can be affected by previous nutrition. There is ample evidence within the literature supporting each of these viewpoints, with seemingly contradictory reports indicating that nutritional treatments such as raising energy intake or decreasing frequency of feeding can increase, have no effect on or decrease the weight of fat in the body of animals compared at a similar weight.

Many of the conflicting reports on the effects of nutrition on body composition could be reconciled if there was precise knowledge of the interrelationships between nutrient intake, stage of animal maturity, and the partition of energy between needs for maintenance, protein synthesis and lipogenesis. There is now sufficient information to define these interrelationships in lambs and to predict the growth and body composition changes associated with various nutritional treatments. In this paper these relationships are used as the basis for speculations on the effects of plane of nutrition, frequency of feeding and protein content of the diet on body composition.

II. BASIS FOR CALCULATIONS

Relationships used to make the predictions were derived from experiments with male crossbred lambs ranging in weight from 3 to 38 kg and fed solely liquid diets of varying protein content at energy intakes from starvation to ad libitum. The major steps in calculating the effects of nutrition on growth and body composition were as follows: (1) calculation of metabolizable energy (ME) intake; (2) partition of ME intake between (i) maintenance net energy, (ii) protein gain, (iii) wool gain, (iv) heat loss associated with maintenance and with production, (v) fat gain; (3) calculation of weight gains in protein, fat, water and ash; (4) calculation of live-weight gain; (5) summation of daily gains in all components to give long term effects of nutrition.

The crux of the calculation was the partition of ME, particularly that for the maintenance requirement of net energy and for protein balance. Maintenance net energy, which is positively related to metabolic weight (Wm, Kg3/4), growth rate and digestible energy intake, and negatively related to age, was calculated from the relationship of N.McG. Graham, T.W. Searle and D.A. Griffiths (prepared for submission to Aust. J. Agric. Res.). Maintenance protein need, which depends upon the intake and biological value of dietary protein, Wm and energy intake, was calculated from the equations of J.L. Black and D.A. Griffiths (prepared for submission to Br. J. Nutr.). The calculations were done by computer, and full details of the computer programmes will be published subsequently. The relationships between...

CSIRO, Division of Animal Physiology, Prospect, P.O. Box 239, Blacktown, 2148.

211
body weight and the weight of fat and protein in male lambs fed reconstituted
dried cow's milk for experimental observations (T.W. Searle and N.McC. Graham
unpublished) are compared in Figure 1 with the computer predictions. Although the
weight of fat tends to be underestimated, the general form of the predicted
relationships closely follows that observed experimentally.

III. PREDICTED EFFECTS OF NUTRITION ON BODY COMPOSITION

(a) Plane of nutrition

(i) Partition of ME intake. The effects of increasing ME intake on the
partition of energy between maintenance requirement, protein and fat deposition,
and heat loss were calculated for lambs weighing 5kg and given an optimal protein
intake (Figure 2 a). At maintenance energy intake (M) there is a gain in body
protein and a loss in body fat; experimental data not used in the calculations
support this prediction (Jordan and Erovm 1970; Jagusch and Mitchell 1971; Walker
and Norton 1971). Further, at ME intakes above 2.2 MJ/d where fat deposition
commences, there is a constant ratio between the increase in fat deposition and
the increase in protein deposition resulting from any specific increase in ME intake.
However, the overall effect of increasing energy intake from maintenance on the
ratio of fat gain to protein gain is curvilinear, approaching an asymptote equiva-
lent to the constant ratio mentioned above (Figure 2 b). The pattern of protein
and fat loss during severe undernutrition is affected by the greatly increased
protein catabolism occurring in lambs near starvation (Figure 2 a). Similar
relationships to Figure 2 for heavier animals show that the relative magnitude of
protein gain and fat loss at maintenance becomes less as body weight increases.
(ii) Predicted growth patterns. The predicted effects of increasing the intake of cows\' milk from 20 to 70 g dry matter (DM)/Wm/d on the amount of protein and fat in the body of a lamb grown from 5 to 18 kg is shown in Figure 3. Increasing the plane of nutrition increases fat deposition at any body weight, but the magnitude of the effect progressively diminishes. In contrast, protein deposition is greatest at the lowest intake, but differences are small and would be difficult to demonstrate experimentally. Predicted growth rates increase from 40 to 390 g/d as DM intake increases from 20 to 70 g/Wm/d. That is, a faster growing animal is fatter at any body weight. The effects of plane of nutrition on body composition decrease as the animals approach mature size. For example, an animal given 70 g DM/Wm/d contains 1 kg (120%) more fat at 16 kg, but only 450 g (45%) more fat at 40 kg than an animal given 25 g DM/Wm/d.

![Fig. 3. Predicted effect of milk intake (g/DM/Wm/d) on body composition of a lamb grown from 5 to 18 kg.](image)

The predicted effects of reducing intake in a lamb which had already grown to 24 kg body weight on a moderately high plane of nutrition is shown in Figure 4. Initially as energy intake is decreased, but maintained high enough to permit weight gain, the amount of fat in the body relative to that in a continuously grown animal progressively decreases. With continued growth on the lower levels of intake, however, the amount of fat in the carcass increases again so that at 40 kg there is little difference due to treatment. In the case of body weight loss, the relationship between body fat and body weight is dependent upon the rate of weight loss. A slow loss results in less fat, a medium loss in the same amount of fat and a rapid loss in more fat than occurs at similar weights during uninterrupted growth. Since data used in the calculations were collected from animals in which the weight loss period did not exceed 14 days, predictions for prolonged weight loss are speculative. There is evidence that both nitrogen excretion (Graham 1967) and metabolic rate (McCance 1972) decline with prolonged undernutrition and body composition may return towards that of animals with uninterrupted growth.

![Fig. 4. Predicted effects on body fat content of reducing the milk intake (g DM/Wm/d) of a lamb weighing 24 kg.](image)
Further calculations suggest (Figure 5) that reduced fat deposition established at low body weights by feed restriction is maintained to high body weights despite subsequent liberal feeding. Conversely, increased fat deposition established at low body weights by liberal feeding is not maintained at heavy body weights when feed is restricted.

(iii) Frequency of feeding. The effects of varying plane of nutrition on body composition suggest that the frequency of feeding may also influence body composition. By reducing meal frequency at a given level of feeding, an animal would effectively be on a higher plane of nutrition immediately following feeding and a lower plane of nutrition prior to the next feed. Depending on the level of intake and the time interval between feeds, this could result in no effect, a slight decline or an increase in the amount of body fat compared with animals of the same weight fed more frequently. If the level of intake is high and the time interval between feeds small, little effect on body composition would be expected from infrequent feeding. This is explained in Figure 2 b if total feed intake is 5 MJ/d, but infrequent feeding effectively causes it to fluctuate between 4 and 6 MJ/d; the increase in fat deposition immediately after a meal is matched by a similar decrease prior to the next meal. Alternatively, if feed intake is low or the interval between feeds is large but the animal is not in a post absorptive state (starved), infrequent feeding would produce a leaner animal. For example, if feed intake is 3 MJ/d (Figure 2 b) but fluctuates from 1.5 to 4.5 MJ/d with infrequent feeding, the increase in fat deposition after one meal is more than matched by an equivalent decrease prior to the next. Further, if the level and frequency of feeding are such that an animal is effectively starved for some period, infrequent feeding results in a fatter animal. In this case, both the higher level of feeding and starvation (Figure 4) result in an increase in fat deposition relative to a frequently fed animal of the same weight.

Calculations suggest that whenever a particular pattern of feeding results in a fat animal, it grows more slowly and retains less nitrogen than a thin animal given the same total feed in a different pattern.

(b) Protein content of diet

(i) Partition of ME intake. The predicted effect of increasing the percentage protein in absorbed nutrients on the partition of energy between maintenance requirement, protein and fat deposition, and heat loss is illustrated in Figure 6 a for a lamb weighing 5 kg and given a constant ME intake. In this calculation it was assumed that the maintenance requirement for net energy was independent of protein intake. As the protein content of the diet increases, the proportion of energy deposited in protein increases to the point where protein intake no longer limits protein synthesis. Thereafter it remains constant. Since there is a
greater heat loss with both high and low protein diets (Hartsook and Hersberger 1971; Walker and Norton 1971), the predicted effect of increasing protein intake on the ratio of fat gain to protein gain is curvilinear; the ratio decreasing rapidly until protein requirement is reached and then only slightly further with excess protein (Figure 6b). Relationships for heavier animals are similar except that protein requirement as a percentage of ME falls as body weight increases.

![Graph showing maintenance, heat loss (maint.), heat loss (prod.), fat, and body protein against protein intake as a percentage of ME.](image1)

Fig. 6.- Effect of increasing protein intake on (a) the partition of ME, (b) the ratio of fat to protein in energy gain of a lamb given 5.3 MJ ME.

![Graph showing predicted effect on body composition of increasing dietary protein content from 6 to 35% of ME in a lamb with a constant ME intake.](image2)

Fig. 7.- Predicted effect on body composition of increasing dietary protein content from 6 to 35% of ME in a lamb with a constant ME intake.

(ii) Predicted growth patterns. The predicted effects of increasing the percentage protein in absorbed nutrients on the amount of protein and fat in the body of lambs given a ME intake of 1.3 MJ/M\(\text{N}\)/d is shown in Figure 7. At this constant energy intake, low protein diets produce a lamb containing more fat and less protein, but the effect diminishes at high protein intakes. Predicted mean growth rate increases from 159 to 329 g/d as the protein content of the diet changes from 6 to 35\% of ME. In this case, a slower growing animal is fatter.

The percentage dietary protein below which a marked increase in body fat content occurs decreases with increasing body weight. For example, with a lamb grown on an adequate protein diet to 30 kg, diets containing 10\% or more of ME
as protein have little effect on body composition.

Voluntary feed intake is commonly reduced when animals are given protein deficient diets (Osborne and Mendel 1916; Egan 1965). This, however, is predicted to produce even more fat in the body (Figure 8). There is an interaction between protein and energy intake and their effect on fat content. Figure 8 illustrates the relationship for a lamb at 20 kg following growth from 9 kg body weight. With diets severely limiting in protein, increasing energy intake reduces body fat. With diets moderately deficient in protein, energy intake has little effect on body fat content, and with diets adequate in protein increasing energy intake increases body fat deposition. The decrease in fat deposition with increasing energy intake is consistent with the finding that lambs fed low protein diets at a maintenance level of energy intake lose protein and gain fat (Walker and Norton 1971). This is opposite to the effect with diets adequate in protein (Figure 2). However, as feed intake is raised to the level where protein deposition commences, there is a constant ratio between the increase in fat deposition and the increase in protein deposition for any specific increase in intake and again the overall effect of increasing energy intake is curvilinear.

IV. DISCUSSION

Although the body composition of animals of a given breed and sex is closely related to body weight, the predictions for lambs presented in this paper suggest that composition can be manipulated by nutritional treatments. The predictions serve mainly to illustrate the principles involved, but they also allow an assessment to be made of the relative importance of various treatments. By altering the intake of diets adequate in protein, the maximum differences in fat deposition are unlikely to exceed 5 to 8% of body weight. At low body weight, however, this can represent more than a doubling of body fat. On the other hand, the differences in fat deposition resulting from alterations in protein content of diets are much greater and theoretically may exceed 50% of body weight. It is clear that the effects of nutrition on body composition are not simple – with interactions between plane of nutrition; chemical composition of the diet, frequency of feeding and stage of maturity of the animals.

Although the predictions are speculative and were based on principles established in experiments with liquid-fed lambs, they do offer some explanation of many observations in the literature. For example, experiments in which the effects of plane of nutrition on body composition were investigated suggest that raising energy intake can increase (Wilson 1968; Morgan 1969; Leche 1970; Lohman 1971; Searle, Graham and O’Callagan 1972; Stahly and Wahlstrom 1973), have no effect on (Reid et al. 1968; Burton and Reid 1969; Murray 1971; Searle et al. 1972; Kellaway 1973) or decrease (Andrews and Grskov 1970; Kellaway 1973) the weight of fat in the body or carcass at a particular body weight. The reports showing either
a positive or no effect of increasing energy intake on body fat content can be explained by the predicted curvilinear relationship between energy intake and fat deposition for diets adequate in protein. This curvilinear relationship has been observed in calves (Morgan 1969). The experiments showing a decrease in body fat with increasing plane of nutrition can be explained by the feeding of low protein diets (Kellaway 1973), or the feeding of diets in which the protein source was extensively degraded within the rumen (Andrews and Ørskov 1970) and in which case increasing energy intake would be expected to stimulate protein absorption to a level that would fulfill the animal's requirements.

Dramatic changes have been noticed in the body composition of lambs (Mitchell and Jagusch 1972; Searle et al. 1972; Kellaway 1973) and rats (Zucker and Zucker 1963) following weaning. The changes are associated with either a loss of or little change in body fat but an increase in body lean. These observations can be largely explained by a decrease in energy intake associated with weaning (Figure 4). Mitchell and Jagusch (1972) and Searle et al. (1972) observed a greater fat loss when intake was restricted after weaning. Furthermore, Young and Sharma (1973) suggest that pigs fed a restricted level of feed in early life and then fed liberally may produce carcasses with less fat than pigs fed liberally throughout, a contention supported by the predictions (Figure 5).

There are a number of contradictory reports on the effects of weight maintenance or loss on body composition. It has been suggested that these treatments result in animals with less fat (Carroll, Peckham and Behnke 1961; Sutterfield 1966; Mendez 1966; Robinson and lambourne 1970; Sebeck 1973), with the same amount of fat (Sebeck and Tulloh 1968; Murray 1971) or with more fat (Mayer and Clawson 1964; Winter 1971) than animals of similar weight grown normally. These differences can be largely explained by the rate of weight loss and the time spent on the treatment. For example, Searle et al. 1972 plotted the fat content of sheep losing weight rapidly and slowly against body weight and showed that, compared with animals grown normally, they contained, respectively, more and less fat; this agrees with the predictions. However, with time, the body composition of both groups of animals returned to that of the normally grown animal.

It has been observed that either decreasing the frequency or altering the pattern of feeding the same total amount of food to rats, mice, chickens or pigs can increase (Cohn 1963; Heggeness 1965; Friend 1967; Fabry and Tepperman 1970; Fowler and Livingstone 1971), have no effect on (Fowler and Livingstone 1971; Braude 1972) or decrease (Friend and Cunningham 1967) the amount of fat in the body or carcass at a particular body weight. These differences are predictable and depend on the level of intake and the interval between meals. The observed increases in body fat content were associated with slower growth rates and greater urinary nitrogen losses, changes that again were predicted. Although the effects of infrequent feeding in ruminants are complicated by the rumen, the principles developed should apply if consideration is given to the absorbed nutrients.

There is considerable support in the literature for the prediction that the feeding of protein deficient diets produces animals with more fat at a given body weight and that the effects become progressively less marked as protein intake approaches requirement (Hamilton 1939; Widdowson and McCance 1957; Robinson, Morgan and Lewis 1964; Norton, Jagusch and Walker 1970; Andrews and Ørskov 1970). The predictions support the contention of Clawson (1965) that animals cannot be forced, by giving excess dietary protein, to produce more lean meat than is permitted by their heredity.

There are limitations to the present predictions. For example, the possible effects of feed restriction in early life on cell multiplication and subsequent permanent stunting with differential development of tissues (Robinson 1971) are not considered. Nevertheless, they can serve as a useful guide for the design and interpretation of body composition experiments and can be of assistance in the
assessment of the relative efficiency of alternative management practices for manipulating body composition.

V. REFERENCES