THE RELATION BETWEEN THE RESPONSES OF WOOL GROWTH AND BODY WEIGHT TO CHANGES IN FEED INTAKE

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Summary

The wool growth responses to changes in feed intake are related to the changes produced in body weight. The relation is expressed by the equation $W = Ei - kC$, where W = wool growth rate, i = feed intake rate, C = rate of body weight change, and E and k are constants. The ratio of E to k in sheep of different productive efficiency was found to be constant.

Evidence is presented that this equation indicates a relation between wool growth and metabolic rate, both possibly being responses to changes in endocrine secretion. An alternative interpretation that the equation reflects the effect of body weight change on the supply of amino acids limiting wool growth is also discussed but is considered less likely to be true.

The bearing of the results on the evaluation of feedstuffs for wool production and on the definition of individual productive efficiency is discussed.

I. Introduction

Both body weight and wool growth rate of adult sheep increase with increasing feed intake above maintenance, but below maintenance loss of body weight contrasts with continuing wool growth (Marston 1948; Ferguson, Carter, and Hardy 1949). The disparity of the two responses to submaintenance feed intakes raises the question of whether or not wool growth can be regarded simply as a constant fraction of the total storage of net energy and likely to respond accordingly to nutritional and other influences which affect energy storage.

Nutritional responses in wool growth are substantially effected by changes in mitotic activity of the follicle papillae (Schinckel 1962) whereas, in the adult animal, changes in body weight in response to changes in feed intake are largely due to alterations in cell size of muscle and fat tissues. The deficit of nutrients required for essential physiological functions, on submaintenance feed intakes, is met, therefore, largely from a decrease in cell size of general body tissues. Indeed a reversal of cell multiplication to provide such needs would be a much more complex process to evolve. The dependence of wool growth on cellular proliferation may partly explain the immunity of wool growth to catabolism and gives further grounds for questioning whether wool growth responds as a constant fraction of net energy storage.

The relative responses of wool growth and body weight to changes in feed intake were examined in the course of an investigation into the influence of thyroxine injections on wool growth (Ferguson 1958) and it was suggested that the

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responses were inversely related and thus consistent with the concept that body tissue changes serve as a source of nutrients for wool growth on submaintenance intakes and reduce the proportion of nutrients available for wool growth on intakes above maintenance. The present investigation was made to examine further the relations between wool growth and body weight change and although similar quantitative results were obtained a fuller discussion of their interpretation is given.

The experimental data employed were taken from an experiment carried out to show whether the wool growth response to increased feed intake was dependent on an increased protein intake (Ferguson 1959). Since no influence of the percentage protein content of the diet on wool growth or body weight was observed, the combined data for the different isocaloric diets have been used in the present analysis.

TABLE 1

COMPOSITION OF EXPERIMENTAL DIETS: PARTS BY WEIGHT

Expt. Period	Diet No.	Lucerne Chaff	Maize	Wheat	Peanut Meal	Wheaten Chaff	Oats	Linseed Meal	Cocoanut Meal	Salt
1–2	F6	50	—	20	—	—	10	10	10	1
3–8	F6	50	—	20	—	—	10	10	10	1
	F11	50	40	—	10	—	—	—	—	0·5
	F12	50	25	—	25	—	—	—	—	0·5
	F13	50	10	—	40	—	—	—	—	0·5
9–10	F11	50	40	—	10	—	—	—	—	0·5
11–13	F11	50	40	—	10	—	—	—	—	0·5
	F14	50	50	—	—	—	—	—	—	0·5
	F15	25	50	—	—	25	—	—	—	0·5
	F16	—	50	—	—	50	—	—	—	0·5

II. MATERIALS AND METHODS

Thirty-six 2-year-old medium-wool Merino ewes were housed in individual indoor pens and fed 500 g daily for 8 weeks. The sheep were then fed *ad libitum* for 12 weeks prior to the intakes being reduced to 500 g per day again and maintained at this level for 32 weeks. The composition of the diets used is set out in Table 1. In those experimental periods where more than one diet was fed, groups of nine sheep each received the different diets as described by Ferguson (1959). The apparent digestibility of energy for diet F11 was determined by Mr. J. C. D. Hutchinson in connection with other experiments. The average values for five determinations each with four sheep fed 600 g per day were 3·98 kcal gross energy per gram and 3·06 kcal digestible energy per gram as fed.

No determinations were made of metabolizable energy but Forbes *et al.* (1928) give an average value for the metabolizability of digestible energy of 83·4% for a diet of 50% lucerne hay and 50% maize fed to steers at levels comparable

to those used in the present experiment. When this factor is applied to the above value of digestible energy, it gives a value for metabolizable energy of $2 \cdot 55$ kcal/g as fed. The different diets used were not significantly different in their effects on body weight so that they may be presumed to have approximately similar contents of metabolizable energy.

The growth of wool was measured at 4-weekly intervals by clipping 10 by 10 cm midside sample areas defined by tattoo lines. The ratio between the sample and total growth of clean wool was determined for each sheep over the
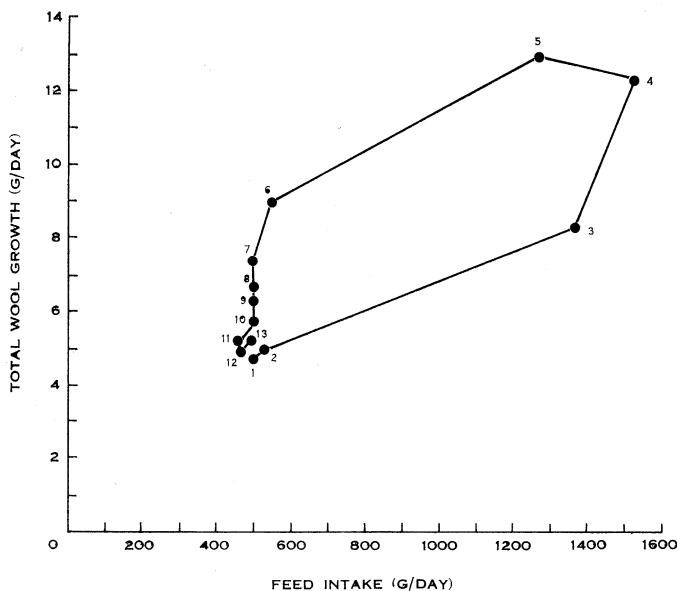

Fig. 1.—Relation of wool growth to feed intake. The numbers opposite the points refer to the successive 4-weekly wool growth periods.

12-week period of *ad libitum* feeding by shearing the sheep at the beginning and end of this period. Further values of this ratio were determined for most of the sheep over a 12-month period at the conclusion of the experiment. These latter values have been used to calculate total wool growth from midside sample values except in nine instances where the later data were not available and the earlier values were used. It has been found that the ratio of total to midside growth is not affected by the feed intake (Ferguson, Carter, and Hardy 1949).

The midside wool samples were extracted successively with ether and water to remove wax, suint, and dirt and the oven-dry weights obtained. The total fleeces were scoured in soap and soda (Chapman 1960).

Environmental temperatures were taken as the mean of daily maximum and minimum air temperature readings in the animal house.

Partial regression analysis was carried out as described by Fisher (1941).

Body weight was measured on Mondays and Thursdays each week and the mean value for each week adjusted for fleece increment before being used to calculate the regression of body weight on time within each 4-weekly wool growth period. The changes from restricted to *ad libitum* feeding and the reverse affected the degree of alimentary fill. The effect of this on the regression of body weight on time within the periods immediately following the changes in feed intake is not likely to be great since the major part of the alimentary adjustment would occur before the first measurement of body weight after the changes. However, feed intake did increase throughout the first period after the change to *ad libitum* feeding so that the estimate of body weight change for this period is likely to be somewhat weighted by an increase in intestinal fill.
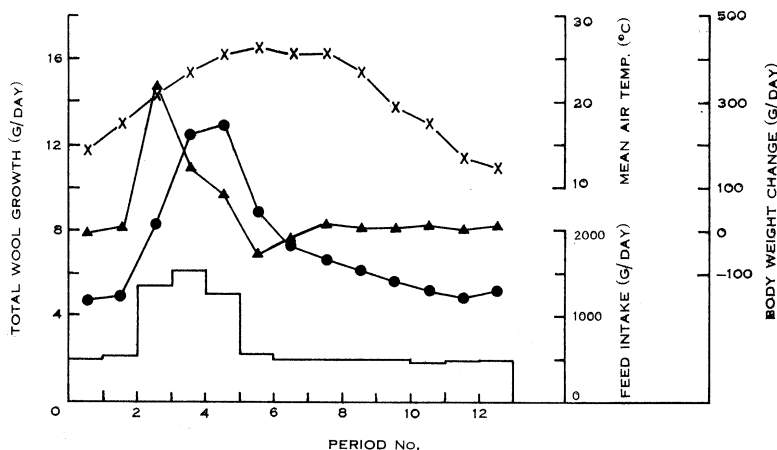

Fig. 2.—Wool growth rate (●——●), rate of body weight change (▲——▲), mean air temperature (×——×), and daily feed intake (——) for each successive 4-weekly wool growth period.

III. RESULTS

The mean wool growth rates for the successive 4-weekly periods are shown plotted against the corresponding feed intakes in Figure 1. It is clear that the wool growth response to changes in feed intake is not immediate, and the quantitative relation between wool growth and feed intake found by Ferguson, Carter, and Hardy (1949) would only be true for closely specified conditions.

The mean wool growth rates and the rates of change in body weight for the different wool growth periods of the experiment are plotted in Figure 2. Mean air temperatures and daily feed intakes for these periods are also included in this figure.

The increase in feed intake produced the greatest effect on body weight in period 3, the response thereafter diminishing while wool growth increased progressively during the three periods of *ad libitum* feeding. Wool growth and body weight change, both expressed per unit feed intake (Fig. 3), move in opposite directions with the changes in feed intake.

The simplest expression of this inverse relation takes the form

$$W/i = E - kC/i, \tag{1}$$

where W = rate of wool growth (g/day), i = feed intake (g/day), C = body weight change (g/day), and E and k are constants. From equation (1) it follows that

$$W = Ei - kC. \tag{2}$$

Such a relation is not apparent from the separate relations of wool growth to feed intake and to body weight change, both of which have positive regression coefficients. Least squares estimation of E and k in equation (2) would seem unsatisfactory in view of the high correlation between feed intake and body weight change, and these constants were therefore estimated by fitting equation (1) to the experimental data.
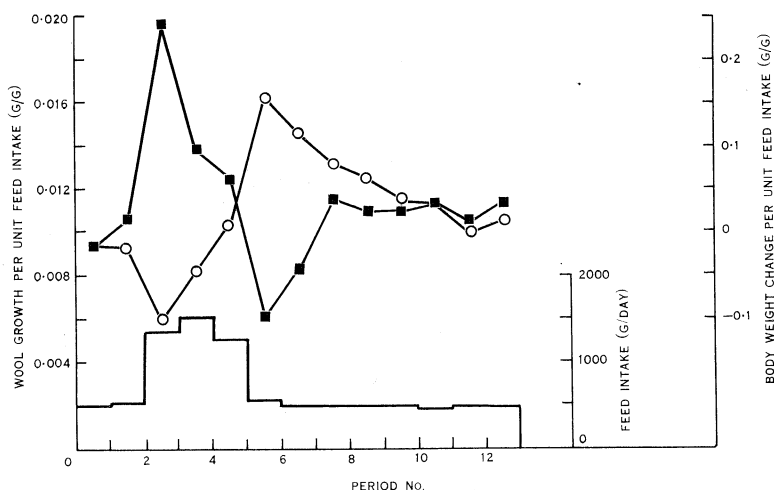

Fig. 3.—Wool growth per unit feed intake (○——○), body weight change per unit feed intake (■——■), and daily feed intake (———) for each successive 4-weekly wool growth period.

Equation (1) does not express or require any fixed relation of body weight change to feed intake, thus allowing for a change of maintenance requirement. In subsequent discussion the observed efficiency of wool growth, W/i, is referred to as gross efficiency, while E, representing that value of W/i when body weight does not change, is referred to as the net efficiency of wool growth.

In fitting equation (1) to the experimental data, terms were included to estimate the seasonal variation in efficiency of wool growth and any possible time trend in efficiency, resulting from increased age of the sheep or possibly from reduced adrenal cortical activity (Lindner and Ferguson 1956) as the sheep became better adapted to their surroundings. The seasonal rhythm in wool growth observed under constant nutritional conditions is empirically more closely related to mean air temperature than to any simple function of day length (Ferguson, unpublished data). This does not demonstrate that variation in temperature is the cause of the

seasonal rhythm in wool growth but it does suggest that mean air temperature is a suitable independent variable to take account of the seasonal rhythm in a partial regression analysis.

On a constant feed intake, the relation of wool growth, and hence efficiency of wool growth, to mean air temperature is linear (Ferguson, Carter, and Hardy 1949). These authors also found some evidence that the regression of wool growth on temperature increased with feed intake. To the extent that the regression coefficient is proportional to feed intake, such an effect is taken care of in the present analysis in which efficiency rather than wool growth is related to temperature.

TABLE 2

REGRESSION COEFFICIENTS OF THE GROSS EFFICIENCY OF WOOL GROWTH ON BODY WEIGHT CHANGE PER UNIT FOOD INTAKE, TEMPERATURE, AND TIME

Values given are the means for all sheep

Independent Variable	Regression Coefficient $\pm$ S.E.
Body weight change (g/g feed intake)	$-0 \cdot 03329 \quad \pm 0 \cdot 003342$***
Mean air temperature (°C)	$0 \cdot 0002754 \pm 0 \cdot 00003285$***
Time (4-week periods)	$0 \cdot 0002437 \pm 0 \cdot 00004381$***

***$P < 0 \cdot 001$.

Partial regression analysis does not accurately measure the separate effects of different independent variables when these are highly correlated with one another. It may be seen in Figure 2 that there is not a high correlation of either mean air temperature or time with body weight change so that the influence of temperature and time can be satisfactorily taken out by partial regression revealing the proper relation between the efficiencies of wool growth and body weight change.

In the partial regression analysis, the mean gross efficiency of all sheep for each wool growth period was related to the mean body weight change per unit feed intake and to the mean air temperature and time for the same periods.

Having adjusted the values of gross efficiency to the mean values of both temperature and time, the relation of the adjusted values to body weight change per unit feed intake was linear apart from one particularly divergent point, representing period 3 when the greatest rate of body weight increase was observed. Since feed intake was increasing throughout this period, it is likely that body weight increase was weighted by an increase in alimentary fill. The value for period 3 being at the extreme end of the scale had an undue effect on the partial regression coefficient for body weight change. This value was therefore omitted and the partial regression coefficients recalculated. They are shown in Table 2.

Gross efficiency, adjusted to the mean values of temperature and time, is plotted against body weight change per unit feed intake in Figure 4. With the exception of period 3, the gross efficiency of wool growth during the experiment is remarkably well predicted from the change in body weight per unit feed intake.

Equation (2) may then be written:

$$W = 0 \cdot 01188i - 0 \cdot 03329C.$$

Change in body weight by 1 g is therefore equivalent to $2 \cdot 8$ g feed intake in effect on wool growth.

Equation (2) might be interpreted as expressing a proportional relation between wool growth and the sum of nutrients obtained from feed intake and body weight change, the latter taking positive or negative values. If this equation expresses the dependence of wool growth on the energy supply from both sources rather than on the supply of a limiting amino acid such as cystine or methionine,
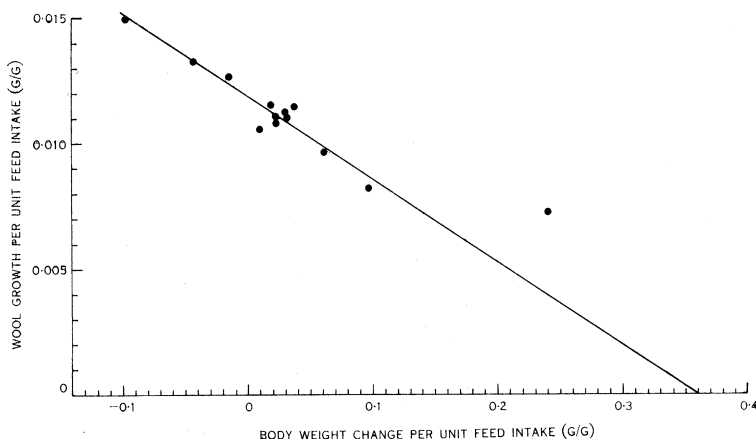

Fig. 4.—Relation of gross efficiency of wool growth (adjusted for temperature and time) to body weight change per unit feed intake. Mean data for all sheep.

then the contribution of body weight change to the energy supply might be expected to be such that k has a value similar to E when feed intake and body weight change are expressed as metabolizable energy intake and change in energy stored, respectively. In other words energy supplied from feed would have the same effect on wool growth as energy from body weight loss. Storage of energy in body weight gain would cause an equivalent loss in wool growth.

Taking the value of $2 \cdot 55$ kcal/g for the metabolizable energy of the diets and $5 \cdot 65$ kcal/g for the energy content of wool the value of E would be $0 \cdot 01188 \times 5 \cdot 65/2 \cdot 55 = 0 \cdot 0263$. The same value of k would be obtained if the calorific value of body weight change were taken as $7 \cdot 1$ kcal/g. Armsby and Moulton (1925) cite the results of various authors on the energy content of body weight gains in sheep during growth and fattening. The values range from $3 \cdot 1$ to $8 \cdot 8$ kcal/g. Keys, Anderson, and Brozek (1955) obtained a value of $6 \cdot 2$ kcal/g of body weight gain in adult humans and Passmore, Strong, and Ritchie (1958)

obtained values between $7 \cdot 0$ and $8 \cdot 1$ kcal/g for body weight lost by obese humans on reducing diets. Thus the value of $7 \cdot 1$ kcal/g is a possible one since a value towards the upper end of the range may be expected from adult sheep in good condition fed diets adequate in protein.

The relative values of E and k are of the right order for wool growth to be considered proportional to the sum of the metabolizable energy of the diet and the energy content of body weight change. The sum of these two energy components is equal to the heat production or metabolic rate plus the amount of energy stored in wool which from the value of k and E in energy terms given above is only $2 \cdot 6\%$ of the metabolizable energy.

TABLE 3

REGRESSION COEFFICIENTS OF THE GROSS EFFICIENCY OF WOOL GROWTH ON BODY WEIGHT CHANGE PER UNIT FOOD INTAKE, TEMPERATURE, AND TIME FOR HIGH-, MEDIUM-, AND LOW-EFFICIENCY GROUPS

Independent Variable	Regression Coefficient $\pm$ S.E.		
	High	Medium	Low
Body weight change (g/g feed intake)	$-0 \cdot 03993$ $\pm 0 \cdot 004380$***	$-0 \cdot 03234$ $\pm 0 \cdot 004618$***	$-0 \cdot 02727$ $\pm 0 \cdot 002489$***
Mean air temperature (°C)	$0 \cdot 0003110$ $\pm 0 \cdot 00004117$***	$0 \cdot 0003044$ $\pm 0 \cdot 00004666$***	$0 \cdot 0002246$ $\pm 0 \cdot 00003022$***
Time (4-week periods)	$0 \cdot 0002753$ $\pm 0 \cdot 00005456$***	$0 \cdot 0002045$ $\pm 0 \cdot 00006238$**	$0 \cdot 0001996$ $\pm 0 \cdot 00004064$***

** $P < 0 \cdot 02$.   *** $P < 0 \cdot 001$.

Such an interpretation is dependent on a relative constancy in the metabolizability of the diet and in the calorific value of body weight change during the experiment. Marston (1948) found that the percentage of the energy intake that was metabolizable was relatively constant in Merino sheep at different levels of intake. During the three successive periods of *ad libitum* feeding in the present experiment the rate of body weight increase fell markedly (Fig. 2). Even if a somewhat lower value for period 3 is taken in accordance with the fit of equation (1) to the data, the range in body weight change is about threefold which is more than can be reasonably accounted for by change in the calorific value of the body weight increase alone. When feed intake was reduced a decreasing body weight loss occurred for two periods followed by a body weight increase in the third period. These changes are even less interpretable in terms of change in the calorific value of the body tissues and it must be concluded that the principal cause of the trend in body weight change both on increasing and decreasing feed intake was a change in metabolic rate.

Since individual differences in wool growth rate are not associated with differences in apparent digestibility (Marston 1948; Ferguson, Carter, and Hardy 1948; Weston 1959), they must reflect differences in the value of E when comparisons are made on maintenance feed intakes. One would expect the value of k to increase in proportion to E, the two components of metabolic rate contributing in due proportion to wool growth.

This question was examined by calculating the mean net efficiency for each of the sheep for the whole experimental period using the value of $k = 0.03329$. The data were ranked in order of net efficiency and formed into three groups of high, medium, and low net efficiency respectively. Partial regression analysis of
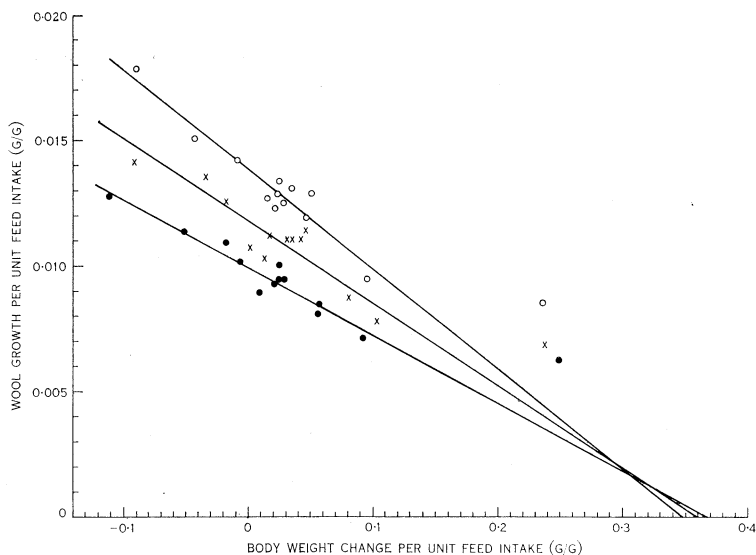

Fig. 5.—Relations of gross efficiency of wool growth (adjusted for temperature and time) to body weight change per unit feed intake for high- (○), medium- (×), and low-efficiency groups (●).

the mean data for each group was carried out using the same independent variables as in the analysis of the mean data for all sheep. The values of the regression coefficients are given in Table 3. The values of k for the three groups are thus 0.03993, 0.03234, and 0.02727 respectively. The corresponding values of E for the data adjusted to the mean values of temperature and time are 0.01386, 0.01171, and 0.00997. The ratios of E to k for the three groups are 0.347, 0.362, and 0.366 showing that k is in fact proportional to E.

The data for the three groups are shown in Figure 5. A consequence of the constant ratio of E to k is that on extrapolation of the lines of best fit they meet on the abscissa at approximately the same point, a body weight change per unit feed intake of 0.36 g per g. This point could not be reached physiologically since it represents zero wool growth with all the metabolizable energy of the feed appearing as body weight increase and none as heat. Thus 0.36 g body weight

change per gram of feed is equivalent in calorific value to $2 \cdot 55$ kcal/g of feed intake which was taken as the metabolizable energy content of the diet.

The constant ratio of k to E is expressed by the equation

$$W/i = E(1 - k'C/i), \tag{3}$$

where $k' = k/E$, and has a value of $2 \cdot 8$ for the conditions of the experiment.

The regression coefficient of gross efficiency on temperature for the mean data is equivalent to a regression coefficient of wool growth (in g/day) on temperature (in °C) of $0 \cdot 138$ for a feed intake of 500 g/day. This compares with values of $0 \cdot 104$ and $0 \cdot 148$ obtained by Ferguson, Carter, and Hardy (1949) for fine-wool Merinos and Corriedales on feed intakes of 500 and 850 g/day respectively of a similar diet to that used in the present experiment.

IV. Discussion

The relation of wool growth to body weight change found in the present investigation indicates that not only does wool growth not form a constant part of the total net energy storage but under some conditions, at least, is inversely related to energy storage and directly proportional to metabolic rate.

The gradual changes in metabolic rate which supervened on changing feed intake may or may not be regarded as changes in the heat increment of feeding depending on the method by which this is determined. However, these changes are unlikely to represent changes in the proportions of acetic, propionic, and butyric acids absorbed but rather alterations of metabolic rate due to endocrine or adaptive enzyme changes. Thus an increase in heat increment associated with more fibrous diets may not have the same effect on wool growth as that observed in the present experiment from an apparent increase in heat production.

Ferguson (1958) found an inverse relation between the efficiencies of wool growth and body weight change when these efficiencies are changed in response to thyroxine injections. The relation found was also represented by the equations applied to the data of the present experiment. Thus the wool growth response to thyroxine is proportional to the changes produced in metabolic rate. However, it has not been established whether the wool follicles share in the general metabolic stimulus of thyroxine or whether the wool growth response results secondarily from an increased metabolic rate. Similarly in the present experiment it has not been shown whether the postulated changes in metabolic rate result from changes in endocrine activity which also affect wool growth or whether the wool growth changes are caused by changes in metabolic rate. In the latter event the stimulus could be transmitted to the follicles by neural or hormonal means, by increased blood flow to the skin, or by an increase in the blood concentration of nutrients limiting for wool growth.

The relation of wool growth to feed intake and body weight change have been interpreted in energy terms on the evidence obtained in the present experiment but reported elsewhere (Ferguson 1959) that increasing the crude protein content of the diet above 8% has no influence on wool growth. However,

Marston (1948, 1955) interprets the wool growth response to increased feed intake as due to an increased supply of amino acids, particularly cystine and methionine, serving as substrate for wool synthesis. Reis and Schinckel (1961) obtained substantial wool growth responses to the administration of casein directly into the abomasum. The responses were in excess of those to be expected from the energy content of the casein administered. Thus the absence of a wool growth response to an increase in the percentage protein of the diet might be explained if the increased protein supplied failed to increase the amino acids available to the animal. Determinations of blood urea made in the present experiment (Ferguson, unpublished data) showed that a substantial proportion of the increased protein supplied must have been lost as urea due to ammonia formation in the rumen (McDonald 1952). If the net synthesis and movement of microbial protein on to the abomasum is more a function of the total feed intake than of the percentage protein of the diet, then the wool growth response to increased feed intake might be interpreted as a response to increased protein reaching the abomasum.

In accord with the latter view, body weight changes might also be interpreted as affecting wool growth by influencing the supply of limiting amino acids. If this were true then the value of k' in equation (3) would be expected to be inversely related to the calorific value of body weight change since the energy content of tissue loss or gain tends to be inversely related to its protein content. Not only is fat of greater calorific value than protein but it is stored "dry" whereas protein storage is accompanied by several times its weight in water. If body weight changes are related to wool growth due to their reflection of changes in metabolic rate or endocrine secretion the value of k' would be directly related to the energy content of body weight change. This alternative interpretation of the experimental results is considered less likely to be true than the interpretation in energy terms, but it cannot be excluded without further investigation.

The results of the present experiment raise the question of evaluation of feedstuffs for wool production. In view of the inverse relation found between wool growth and energy storage, it cannot be assumed that the net energy for fattening, generally used for the evaluation of feedstuffs for different productive purposes, does measure the relative values of feedstuffs for wool growth. If the suggested relation of wool growth to metabolic rate extends to the situation where metabolic rate is raised by feeding diets with a high heat increment, then heat increment rather than energy storage would measure the value of feedstuffs for wool growth. The influence on wool growth of an increased metabolic rate resulting from muscular activity or exposure to cold similarly cannot be assessed from the present experiment. Furthermore under these conditions increased adrenocortical activity may suppress any rise in wool growth (Lindner and Ferguson 1956).

The relations expressed in equation (3) and illustrated in Figure 5 have a bearing on the definition of individual wool growth productivity. Since feed supplies, though varying with season and degree of pasture improvement, are fixed by grazing area, the gross efficiency of wool growth of a sheep will measure its contribution to the capacity of the flock to grow wool from a given pasture area. Variation in gross efficiency is associated with variation in net efficiency

and with variation in body weight change per unit feed intake. The latter component of variation in turn is made up of variation in feed intake and variation in maintenance requirements. Thus the combination of characteristics leading to the highest value of gross efficiency would be high net efficiency, high maintenance requirement, and low feed intake. However, since body weight gain has value as an energy source in subsequent submaintenance feed conditions or in carcass returns the net efficiency of wool growth, by giving due allowance for the wool growth equivalent of body weight change, appears to be a better measure of productivity than gross efficiency.

In addition to wool grown per unit feed supply economic returns are influenced by the number of sheep required to produce the wool since part of total costs are proportional to sheep numbers. Hence a capacity for a high feed intake may be a factor in individual productivity in addition to a high net efficiency of wool growth. However, this factor may be offset if returns from surplus stock are increased with sheep numbers. The best combination of biological characteristics constituting individual wool growth productivity is thus closely dependent on environmental and economic factors.

V. ACKNOWLEDGMENTS

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