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THE DIVISION OF ENERGY DURING GROWTH

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OPSOMMING: DIE VERDELING VAN ENERGIE TYDENS GROEI

Metings op 3 hamellammers in 'n kaloriemeter het ooreengestem met beramings van proteïen- en vetneerlegging wat met behulp van die tritiumverdunningstegniek gemaak is en het gestrek vanaf digby geboorte tot naasteby 36 weke. Die 3 vleismerino hameltjies is deurentyd gedurende alternerende weke of in die kaloriemeter of 'n soortgelyke struktuur aangehou.

Lineêr onafhanklike metings van voedselinname, hitteproduksie, proteïen- en vetneerlegging gedurende die aktiewe groeiproses wys dat die kumulatiewe vorm van hierdie veranderlikes paarsgewys loglineêr verwant is vir elke lam op sodanige wyse dat die tweedimensionele verwantskappe veralgemeen na 'n reguit lyn in 4 dimensies. Die parameters van hierdie reguit lyn is verwant aan die konstante wat groeitempo beskryf en dui daarom op die moontlikheid van verbeterde kwantitatiewe beheer van liggaamsamestelling deur innamebeheer.

Hoofkomponentanalises steun die ekstrapolasie na 'n reguit lyn in 4 dimensies omdat gemiddeld 'n grootste wortel van 99% verkry is. Kumulatiewe voedselinname word teenoor tyd beskryf deur 'n eerste orde outoregressiewe proses met betrekking tot ln (kumulatiewe VE-inname). Kumulatiewe ME-inname, kumulatiewe hitteproduksie, liggaamsproteïen en -vet, word almal loglineêr beskryf deur gewone regressie-analise met kumulatiewe VE as X-veranderlike. Deur van hierdie verwantskappe gebruik te maak, is beramings van die doeltreffendheid van neerlegging vir beide proteïen en vet verkry. Hoewel die bruto doeltreffendheid van energieneerlegging naasteby konstant is oor 'n groot gedeelte van 'n lam se leeftyd, word dit bewys dat sodanige aanname nie geldig is vir die biologiese doeltreffendhede van proteïen en vetneerlegging nie. Beide die dimensie en kurvilineêriteit van die relevante onderlinge verwantskappe het tot gevolg dat die konvensionele gebruik van meervoudige regressiemetodes ongeldig is vir die beraming van parsiële doeltreffendhede van proteïen- en vetneerlegging. Gevolglik word die bestaan van konstante doeltreffendhede *in vivo* van proteïen- en vetsintese betwyfel.

SUMMARY:

Three wether lambs of the Mutton Merino type were kept in confinement in metabolism cages confined to either a calorimeter or a structure resembling the plant, from about birth to about 36 weeks. Measurements over regular intervals with aid of the tritium dilution technique were in agreement with protein and fat retention measured during alternate weeks in the calorimeter.

Linearly independent measurements of feed intake, heat production, protein and fat during active growth indicate that cumulative feed intake, cumulative heat production, body protein and body fat are pairwise log-linearly related for each lamb, in such a fashion that the two-dimensional relationships extend to a straight line in 4 dimensions. The parameters of this straight line determine the growth rate constant for all these traits up to a multiplicative constant with time dimension. This suggests improved quantitative control of body composition by control of feed intake.

Principal components analyses support the extrapolation to a straight line in 4 dimensions by giving, on the average, a first root of 99%. Cumulative feed intake against time is described by fitting first order auto-regressions of ln (cumulative DE intake). In the feed domain, cumulative ME intake, cumulative heat production, body protein, body fat and body mass are log-linearly related by ordinary regression methods to cumulative DE intake. From these relationships efficiencies for protein and fat deposition are calculated and it is shown that the gross efficiency of energy deposition is, approximately, constant over much of a lamb's growth period, while no such constancy can be assumed for the biological efficiencies of protein and fat deposition. Both the dimension and curvilinearity of the system of relationships between the relevant variables invalidate the use of conventional multiple regression methods to calculate partial efficiencies of protein and fat deposition. Consequently, doubt is expressed about the existence of constant efficiencies of protein and fat synthesis *in vivo*.

In a paper by Roux (1976), a pattern of energy division during growth was postulated which follows from pairwise log-linear relationships between cumulative feed intake, cumulative heat production, protein and fat. It was, furthermore, assumed that these linear relationships in 2 dimensions can also be described in 4 dimensions by a straight line instead of a plane or, to be more exact, a 3 dimensional hyperplane.

To fix ideas on the difference between these 2 generalisations to 4 dimensions let

x_1 = ln (cumulative feed intake)
x_2 = ln (cumulative heat production)
x_3 = ln (body protein)
x_4 = ln (body fat),

and let

$$x_i = a_i + b_i x_1 \quad \text{for } i = 2, 3, 4 \tag{1}$$

be the linear relationship between x_2, x_3 and x_4 on the one hand and x_1 on the other hand. Then a straight line in 4 dimensions can be written as

$$x_1 - \alpha_1 = (x_2 - \alpha_2)/b_2 = (x_3 - \alpha_3)/b_3 = (x_4 - \alpha_4)/b_4 \tag{2}$$

where $a_i = \alpha_i - b_i \alpha_1$, as follows from the correspondences between (1) and (2). A 3 dimensional hyperplane in 4 dimensions can be written as

$$x_1 = d_1 + d_2 x_2 + d_3 x_3 + d_4 x_4 \tag{3}$$

For practical purposes the difference between the straight line (2) and the plane (3) is that once the parameters of (2) and (3) (the d_i–s, α_i–s and b_i–s) are known, knowledge of one linear component implies knowledge of the whole system in the situation of (2), but that in the situation of (3) knowledge of 3 components are necessary before the fourth is determined.

The hypothesis of a single dimensional log-linear relationship between cumulative feed intake, cumulative heat production, protein and fat in the body, can be tested by a principal component analysis, which should result in one nonzero root, with the other roots approximately equal to zero.

The ideas discussed thus far are mathematically in a one-to-one relationship with Hopkins' (1966) definition of multivariate allometry. The single dimensional nature of the hyperplane in 4 space, describing growth input and output, reflects the law of conservation of energy and the relative constancy of energy division between the different body constituents and heat production (on the logarithmic scale of measurement) during growth.

Initially, it seems curious that the assumption of (2) allows the derivation of

$$x_1 = a + \{b_2/(b_2^2+b_3^2+b_4^2)\}\, x_2 + \{b_3/(b_2^2+b_3^2+b_4^2)\}\, x_3 + \{b_4/(b_2^2+{}_2^2+b_4^2)\}\, x_4 \tag{4}$$

which can be shown to be a unique relationship (within a well defined system of equations) relating input and outputs. According to Roux (1976, 1981) (4) is the equation reflecting the law of conservation of energy. The proof follows from taking differentials in (4) and from substituting $dx_i = b_i dx_1$, which follows from (1), to obtain an identity.

Writing $y_i = \exp(x_i)$, $i = 1, 2, 3, 4$, (4) detransforms to the arithmetic scale:

$$y_1 = A y_2^{\,b_2/(b_2^2+b_3^2+b_4^2)}\, y_3^{\,b_3/(b_2^2+b_3^2+b_4^2)} \times y_4^{\,b_4/(b_2^2+b_3^2+b_4^2)}. \tag{5}$$

Equation (5) is a unique multivariate allometric relationship between the input and all outputs during growth.

Evidence is provided in Roux (1981) that the relationship of each of the x_i against time can be written in difference equation or autoregressive form

$$x_i(t) - \alpha_i = \rho(x_i(6-1) - \alpha_i) + \varepsilon_i(t) \tag{6}$$

for $i = 1, 2, 3, 4$,

where $x_i(t) \to \alpha_i$ for $t \to \infty$ and where $\varepsilon_i(t)$ are random disturbances and ρ is the autoregressive coefficient. Let $\gamma = -\ln\rho$. Roux (1976, 1981) derives the growth rate constant

$$\gamma = c(1 + b_2^2 + b_3^2 + b_4^2), \tag{7}$$

where c is a constant with time dimension and the b_i – s are the regression coefficients in (1). Since body mass is allometrically related to its chemical constituents (Tulloh, 1963; Elsley, McDonald & Fowler, 1964; Meissner, Roux & Hofmeyr, 1975) it follows by theory and direct observation that, excluding measurement error, (6) also holds for x_5 = ln(body mass). Hence the importance of (7) derives from the fact that it forms a connection between growth rate and the partitioning of energy into heat production and the deposition of protein and fat.

Equations (6) and (7) reflect the control of growth rate by feeding rate, and moreover can serve to influence body composition in a predictable fashion. Since the derivation of (7) follows from the assumption of a single dimension for the four-space describing growth input and output, it seemed worthwhile to put it, and other principles involved, to a critical test in growing lambs by measuring *every* input-output variable independently, and nearly continuously, from birth to approximate maturity.

Material and Methods

Design

Three wether lambs of the Mutton Merino type were kept in confinement from about birth to a body mass of 56 ± 4,8 kg – a life span lasting approximately 35 weeks. During the entire period they were housed and fed within metabolism cages confined to either an open circuit respiration plant or a dummy structure resembling the plant. Body mass, voluntary feed consumption, body composition (protein and fat) and heat production were continuously measured.

Experimental routine

The lambs were taken from their mothers 2 days *post natally,* castrated with elastrator rings and immediately introduced to their metabolism cages and respiration plant or dummy structure. The additional housing facility was necessary because the respiration plant only consists of 2 chambers. Thus, 2 dummy chambers were constructed with exactly the same inner measurements, colour and fan noises, but without respiratory measurement facilities. To avoid drastic environmental changes, both the chambers and the room in which the chambers were housed were maintained at the same temperature of 24 ± 2°C.

The lambs were trained to bottle feeding in the chambers. Cow's milk was supplied according to a schedule employed by Meissner, Roux & Hofmeyr (1975). Milk feeding was continued until the intake of a pelleted growth diet shown in Table 1 was sufficient to limit the effects of abrupt weaning (at about 9 weeks of age). From 3 weeks of age the lambs had free access to the pelleted diet and water. Fresh food was supplied twice daily to provide for *ad libitum* feed intake.

Voluntary intake of digestible (DE) and metabolizable energy (ME) was measured, every week in the case of DE and every fortnight in the case of ME. Body mass was also determined every week. Heat production and body composition were measured every fortnight. Gas exchange, faeces and urine collections were done over six-day periods and corrected to 7 days. On the seventh day body mass and tritiated water space (body composition) were measured, whereafter the lambs were interchanged between the respiration and dummy chambers – the lamb(s) kept in the respiration chambers for a specific week were replaced by the lamb(s) in the dummy chambers, the first mentioned then being introduced to the dummy chambers.

Table 1

Composition of the pelleted diet on an air dry basis

Component	Percentage
Lucerne meal	50
Maize meal	38
Fish meal	10
Monosodium phosphate	1
Calcium carbonate	0,5
Salt	0,5
Commercial mixture of vitamines and minerals	0,1

Apparant metabolisable energy (MJ/kg) = 9,4
Apparent crude protein (%) = 16,2

Animal health

The lambs used were apparently more sensitive and prone to bacterial infections than others not kept in confinement. In fact, 6 lambs were started on the experiment of which only 3 completed the total period successfully. The other 3 died of acute pneumonia relatively early during the experiment. Thus, intensive care of the remaining lambs was called for. The procedure adopted was to measure rectal temperature every morning and to act immediately if alterations occurred. In such cases a course of broad spectrum antibiotics was given and continued for 2 days following the return to normal of the rectal temperature. These methods proved effective, because the growth rate and voluntary feed intake of the experimental lambs compared favourably with those of other lambs not in confinement (Table 2). In addition to the periodic antibiotic treatment, the lambs were also treated twice against enterotoxaemia and internal parasites.

Table 2

Intake and bodymass gain of the lambs in confinement as compared at 2 body masses to lambs not in confinement

Body mass (kg)	In confinement		Not in confinement	
	Intake (MJ/day)	gain (g/day)	Intake (MJ/day)	gain (g/day)
25	11,3 ± 0,84	294 ± 38,5	11,7 ± 1,29	290 ± 73,2
40	13,3 ± 1,50	232 ± 42,4	13,0 ± 0,91	220 ± 56,7

Measurements and techniques

The open circuit respiration plant used to measure gas exchange is described by Meissner (1977) and is based on the same principles as the plants described by Thorbek & Neergaard (1970) and Sundstol, Ekern & Haugen (1974). The composition of air (O_2, CO_2 and CH_4) is measured by continuously collecting aliquots of incoming and outgoing air in specially devised plexiglass receptacles as described by Thorbek & Neergaard (1970). These aliquots, collected over periods of 24 hours, are analysed at the end of a particular collection period by means of a Beckman Model IR 215 B infra-red CO_2 and CH_4 analyser and a Servomex OA 184 paramagnetic O_2 analyser. Heat production is calculated by the formula given by Blaxter & Boyne (1970).

Nitrogen determinations on milk, feed, faeces and urine were performed by macro-Kjeldahl technique (A.O.A.C., 1970). Energy of combustion of milk, feed, faeces and urine was determined with an adiabatic bomb calorimeter. The dry matter in the feed and faeces was determined by drying to constant mass at 100°C in a forced draught oven, while the dry matter in milk and urine was established by desiccation in a vacuum oven.

Protein and fat in the lamb body were calculated from tritiated water space (TOH) using the tritium dilution technique as described by Meissner & Bieler (1975). The prediction equations of Meissner & Bieler were, however, altered slightly because it was found that they predict with marked bias at the extremes. The altered equations were:

(a) before weaning

$$\text{Protein} = 0{,}1732\ \text{TOH}$$

$$\begin{aligned}\ln(\text{Fat}) = {} & 16{,}87 \ln(\text{Body mass}) \\ & 14{,}49 \ln(\text{TOH}) - 10{,}58\end{aligned}$$

(b) after weaning

$$\text{Protein} = 0{,}1984\ \text{TOH}$$

$$\begin{aligned}\ln(\text{Fat}) = {} & 7{,}305 \ln(\text{Body mass}) \\ & 6{,}098 \ln(\text{TOH}) - 6{,}610.\end{aligned}$$

Rates of protein and fat deposition were also calculated from the calorimetric data. Protein deposition was calculated from nitrogen balance. Fat deposition was obtained by subtraction of heat production and protein deposition from ME intake.

Adjustments and assumptions

Experimental design and facilities allowed some measurements, for example ME, to be taken only on alternate weeks. Hence data for the missing weeks were obtained by linear interpolation where need existed.

At any stage of development, body mass is the result of total feed intake up to that point. Thus, in a situation where the relationship of cumulative intake and body mass is examined, it would be erroneous to allocate zero intake to the body mass at first measurement. In this experiment the first measurement was at one week of age. Total ME intake until first measurement was calculated as the amount of energy in the lamb body (Meissner, de la Rey, Gerhard & Van der Westhuizen, 1976) times 100/81, where 81% represents the efficiency of ME utilisation in the newborn lamb (Kielanowski, 1965). Body energy times 19/100 was credited to pre-experimental heat production.

Statistical methods

With careful experimentation measurement error and waste in feed intake is negligible. Since cumulative DE intake was measured most frequently and shows the greatest range (and number of observations) it is best qualified to be the independent variable in ordinary regression analysis for which negligible measurement error is a requirement. A sizeable range in the independent variable reduces bias in the estimation of regression coefficients, because the effect of measurement error becomes negligible.

Hence the pattern in the statistical methods is one of regression analyses with ln (cumulative DE intake) as independent variable. All other regression equations are then obtained by algebraic substitution. This is equivalent to using ln (cumulative DE intake) as instrumental variable (Kendall & Stuart, 1973). With the high correlations obtained in the present set of data (vide tables 5 and 6) this can be expected to be a highly efficient procedure.

Relevant plots of the data showed no serious deviations from the assumptions necessary for valid statistical analysis. The most important property required was a random distribution of points around the straight lines, although some secondary emphasis was also placed on homogeneity of the errors along the lines.

In agreement with the usual statistical procedure common slopes and intercepts are fitted when possible. When the analysis of covariance indicated a common slope, but different intercepts, conditional intercepts were calculated based on the value of the common slope.

Results

The relationship between DE and ME

The cumulative nature of measurement error in ME, makes it necessary to do calculations on differences. The results in table 3 are obtained by the deletion of the points before weaning, which do not show the same relationship as the others. There are no significant differences in slope between the lambs, and the common slope is significantly different from one. Hence the relationship between DE and ME is of the form cumulative ME = A (cumulative DE)^{0,95}, where A is a constant depending on the initial values A = exp a = exp {ln(cumulative ME (0)) − b ln (cumulative DE (0))}, where cumulative ME (0) is the cumulative ME at time zero, and likewise for cumulative DE. The observations for lamb W_{15} are given in Fig. 1.

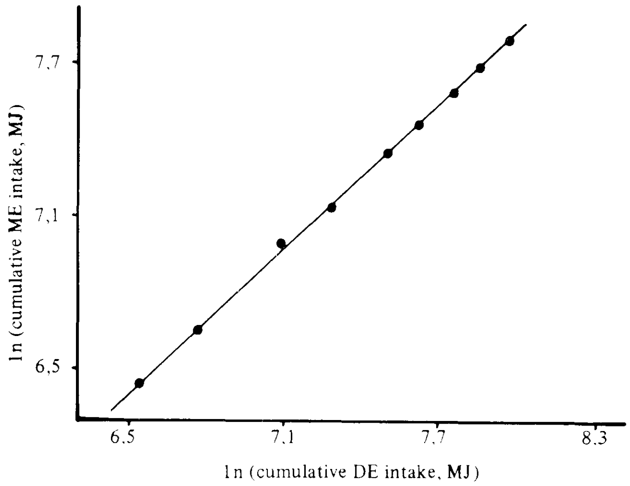

Fig. 1 *The relationship between ln (cumulative DE intake, MJ) and ln (cumulative ME intake, MJ) for lamb W_{15} after 13 weeks of age*

Table 3

Regression relationships between ln(cumulative ME, MJ) and ln(cumulative DE, MJ)

(a) Intercepts and slopes			(b) Tests		
Sheep No.	a	b	Hypothesis	d.f.	F or t
K_1	0,2111	–	$b_1=b_2=b_3$	2;26	0,25
W_{15}	0,2395	–	b = 1	28	8,43**
W_{25}	0,2272	–	s.e.(b) = 0,0058		
Common	–	0,9510	residual s.d. = 0,0067		

Table 4

Regression relationships between measurements in the calorimeter and those based on tritiated water space

Trait	b	s.e.	hypothesis	t-value	d.f.	residual s.d.
ln(protein, kg)	0,954	0,0838	b = 1	0,549	20	0,0387
ln(fat, kg)	0,866	0,1198	b = 1	1,122	19	0,1505

The relationship between measurements in the calorimeter and those on tritiated water space

The tests in Table 4 are again on differences, according to the error structure arising from cumulated calorimeter measurements. The tests are based on the assumption that measurements based on tritiated water space are correct, and the starting values for the calorimeter measurements are those of tritiated water space. No significant deviations from a slope of one were found, and hence the 2 types of measurements are in agreement.

The relationship between input and outputs

The relationships between ln (cumulative DE) and the logarithms of body protein and body fat as based on triated water space, and cumulative heat production

Table 5

Regression relationships with ln(cumulative DE, MJ) as independent variable before 13 weeks

Sheep no.	intercept	s.e. of intercept	slope	s.e. of slope	r^2 and residual s.d.
(a) ln (body mass, kg)					
K_1	–0,9249	0,0312	–	–	
W_{15}	–0,8152	0,0356	–	–	
W_{25}	–0,8858	0,0293	–	–	
Common	–	–	0,6233	0,0141	0,9824 0,0716
(b) ln (cumulative heat production, MJ)					
K_1	–1,0416	–	–	–	
W_{15}	–1,0661	–	–	–	
W_{25}	–1,0646	–	–	–	
Common	–	–	1,0709	0,0280	– 0,0318
(c) ln (body protein, kg)					
Common	–2,7093	0,2686	0,6713	0,0456	0,9558 0,0754
(d) ln (body fat, kg)					
Common	–6,5848	0,5725	1,1162	0,0973	0,9294 0,1607

Table 6

Regression relationships with ln (cumulative DE, MJ) as independent variable after 13 weeks

Sheep no.	intercept	s.e. of intercept	slope	s.e. of slope	r^2 and residual s.d.
(a) ln (body mass, kg)					
K_1	–0,0278	0,0096			
W_{15}	–0,0934	0,0105			
W_{25}	–0,1318	0,0133			
Common	–	–	0,5078	0,0056	0,9917 0,0222
(b) ln (cumulative heat production, MJ)					
K_1	–0,7885	–			
W_{15}	–0,7673	–			
W_{25}	–0,7627	–			
Common	–	–	1,0297	0,0089	– 0,0082
(c) ln (body protein, kg)					
K_1	–0,6511	0,0244			
W_{15}	–0,7098	0,0271			
W_{25}	–0,8099	0,0296			
Common	–	–	0,3515	0,0157	0,8176 0,0401
(d) ln (body fat, kg)					
K_1	–6,9200	0,0448			
W_{15}	–7,0527	0,0523			
W_{25}	–6,9161	0,0856			
Common	–	–	1,1789	0,0308	0,9826 0,0786

before and after 13 weeks are given in tables 5 and 6 respectively.

The need for separate relationships before and after 13 weeks is in agreement with Meissner, Roux & Hofmeyr (1975) and is especially clear in the case of protein and body mass and is a little less pronounced in the case of fat. The relationships after 13 weeks are illustrated by the observations on W_{15} in Fig. 2.

Autoregressive relationships

Only DE was measured extensively and with small enough measurement error for the use of (6). The results are given in Table 7. The distance or β_1 follows from the solution to (6),

$$E\{x_1(t)\} = \alpha_1 - \{\alpha_1 - x_1(0)\}\rho^t \qquad (8)$$

$$= \alpha_1 - \beta_1 \rho^t$$

The adequacy of the model of eq. (6) is tested by a model

$$x_1(t) = a + \Theta_1 x_1(t-1) + \Theta_2 x_2(t-2) + \varepsilon(t) \quad (9)$$

If (6) is adequate, Θ_2 should be nonsignificant. The t-values for Θ_1 and Θ_2 are given in Table 8. Θ_2 is significant only for K_1. This result is atypical for this type of sheep and diet and is due to a small change in intercept in the course of the experiment resulting from some disturbance or other in feed intake. The change in intercept is illustrated in Fig. 3 in the autoregressive plot for K_1

Table 7

Autoregressive relationships for ln (cumulative DE, MJ), measured weekly

Sheep No.	limit (α_1)	s.e.	autoregressive coefficient (ρ)	s.e.	distance (β_1)	residual s.d.
(a) Before 13 weeks						
K_1	–	–	–	–	3,6345	–
W_{15}	–	–	–	–	2,9400	–
W_{25}	–	–	–	–	3,5246	–
Common	7,1533	0,1534	0,8715	0,0117	–	0,0548
(b) After 13 weeks						
K_1	8,5603	0,0623	–	–	2,1421	–
W_{15}	8,4022	0,0623	–	–	1,8479	–
W_{25}	8,2668	0,0639	–	–	1,5979	–
Common	–	–	0,9374	0,0031	–	0,0118

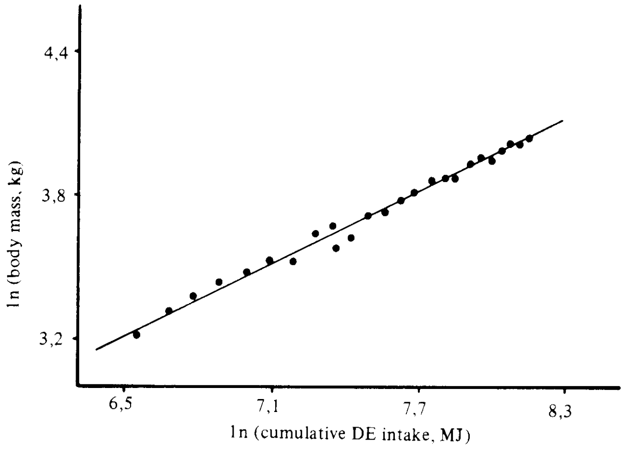

Fig. 2(a) *The relationship between ln (cumulative DE intake) and ln (body mass) for lamb W_{15} after 13 weeks of age*

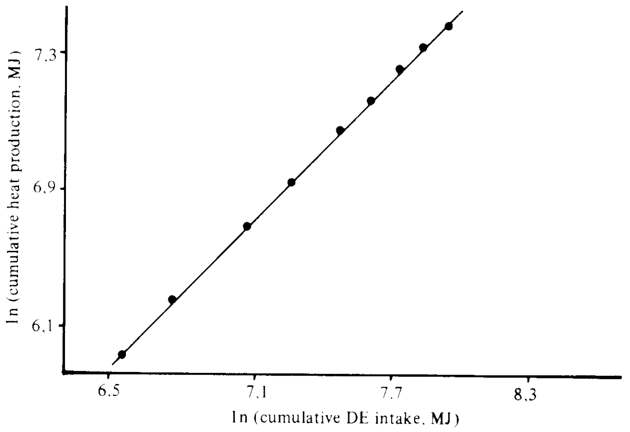

Fig. 2(b) *The relationship between ln (cumulative DE intake) and ln (cumulative heat production), for lamb W_{15} after 13 weeks of age*

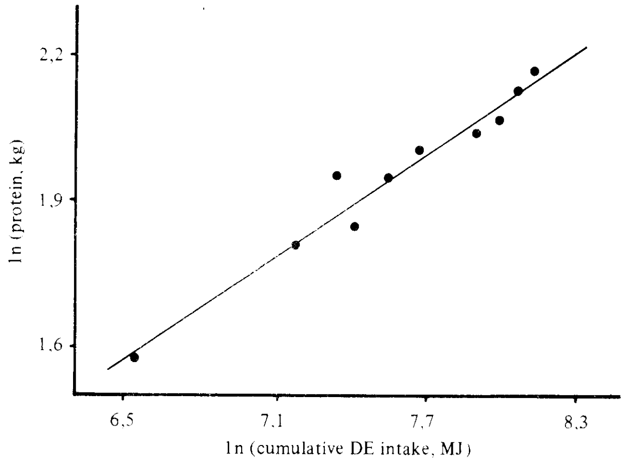

Fig. 2(c): *The relationship between ln (cumulative DE intake) and ln (body protein) for lamb W_{15} after 13 weeks of age*

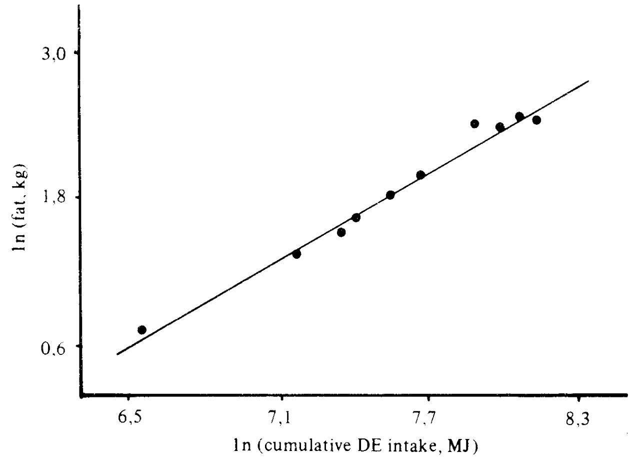

Fig. 2(d): *The relationship between ln (cumulative DE intake) and ln (body fat) for lamb W_{15} after 13 weeks of age*

Table 8

Tests of significance for regression coefficients in second order autoregressive model

Sheep No.	Error d.f.	t_1	t_2
K_1	23	3,74**	2,91**
W_{15}	23	4,94**	–0,60
W_{25}	20	2,89**	1,54

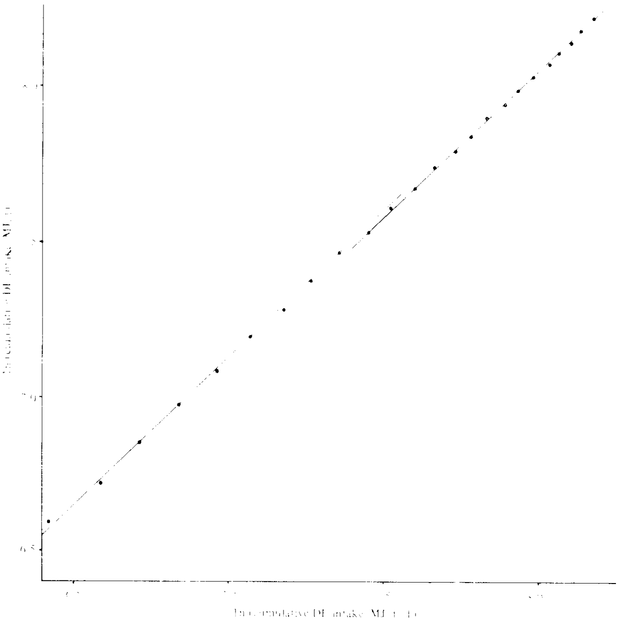

Fig. 3: *The autoregressive plot for ln (DE(MJ)) for lamb K1 after 13 weeks of age*

Table 9

Principal component analysis: the percentage values of the latent roots of the covariance matrix of the logarithms of cumulative digestible energy intake, body protein, body fat and cumulative heat production

Sheep	No.of observations	Largest root	Second root	Third root	Smallest root
K_1	8	99,34	0,62	0,04	0,00
W_{15}	7	99,12	0,73	0,15	0,00
W_{25}	6	99,33	0,56	0,11	0,00
Common	21	99,01	0,88	0,11	0,00

after 13 weeks of age, where $x_1(t-1)$ is represented on the X-axis and $x_1(t)$ on the Y-axis. Such a change in intercept is in line with theory (Roux, 1976).

Principal component analysis

The critical test for the single dimensional nature of the input-output system in four-space describing growth follows from the calculation of the latent roots (eigen values) of the covariance matrices of the lambs K_1, W_{15} and W_{25} after 13 weeks. The roots are shown in Table 9.

Discussion

Dimension of the input-output system

Without measurement error the covariance matrices of ln (cumulative DE intake), ln (cumulative heat production), ln (protein) and ln (fat) would have, under the single dimensional hypothesis, one nonzero root and 3 zero roots. Measurement error causes a positive shift in the zero roots. The results in Table 9 show that the first root contains 99% of the total variation of the 4 variables included in the covariance matrix, and all the other roots contain 1%. Hence 99% of the total variation in the input and outputs can be ascribed to a single dimensional linear relationship between them. The other 1% is small enough to be ascribable to measurement error.

A procedure that may result in a root near to zero would be to obtain, say, heat production by subtracting energy retention from ME intake. Such an artifact of measurement is impossible with the procedures followed here, since 4 characteristics were measured independently to obtain the input and outputs of growth.

Hence the use of eq. (7) offers promise of increased quantitative control of growth rate and body composition by the manipulation of feed intake. The gains in the economy and extent of description of growth should be evident from the results presented.

The efficiency of deposition of protein and fat

In the present context the natural way to define and calculate the efficiences of protein and fat deposition are from the partial derivatives of equation (5). By the use of the relationship

$dy_i/y_i = dx_i$,
$i = 1,2,3,4$ where the index i indicates the same traits as in (1), it follows from (4) that

$$\Delta y_1 = (b_2^2+b_3^2+b_4^2)^{-1} \{(b_2y_1/y_2)\Delta y_2+(b_3y_1/y_3)\Delta y_3 + (b_4y_1/y_4)\Delta y_4\} \qquad (10)$$

since $\Delta y_i = dy_i$, approximately.

Hence it is clear that

$b_iy_1/y_i(b_2^2+b_3^2+b_4^2)$, $i = 2,3,4$, represent the feed conversion ratios for heat production, protein and fat. The partial efficiencies would be equal to

$$y_i(b_2^2+b_3^2+b_4^2)/b_iy_1. \qquad (11)$$

A comparison of (10) with the so-called total differential identifies the feed conversion ratios with partial derivatives, in which, for example protein and ME intake are allowed to vary, but heat production and fat are kept constant.

One might, of course, argue that the assumption of keeping heat production constant is unrealistic, since increases in protein and fat deposition must, necessarily, be associated with increases in heat production. A possible solution to this problem is to consider, analogously to (4) and (5), a relationship including protein and fat only, deleting heat production. It is then possible to calculate derivatives in which only protein or fat, as the case may be, are kept constant. The conversion ratios for protein and fat are then

$$b_iy_1/y_i(b_3^2+b_4^2)$$

for $i = 3,4$ and the partial efficiencies would be equal to

$$y_i(b_3^2+b_4^2)/b_iy_1, \qquad (12)$$

for $i = 3,4$.

Gross efficiency might also be of some interest. In the same form as (11) and (12) the gross efficiencies are

$$dy_i/dy_1 = b_iy_i/y_1, \qquad (13)$$

for $i = 3,4$.

It is, perhaps, worthy of note that all the efficiencies have the same general form

$$y_i(b_i+k)/y_1, \qquad (14)$$

where, for example, k is equal to

$(b_2^2+b_4^2)/b_3$ or b_4^2/b_3 or 0,

for protein, $i = 3$, say. Any efficiency for protein will depend, as regards constancy, on the ratio y_3/y_1. This ratio can only be constant if $b_3 = 1$. From Table 6, $b_3 \neq 1$ and $b_4 \neq 1$, significantly so in agreement with Meissner (1977) with much more extensive data. Hence the conclusion is inescapable that no constant partial efficiencies can be calculated by the methods employed here. Thus, it is a peculiarity of biological organisation that there can be no constant biological efficiencies of protein and fat deposition. Partial support for this fact follows from the conclusion of Kotarbinska & Kielanowski (1967) that protein synthesis in older animals is less efficient than in young ones, and from the great variability of estimates published in the literature, all of which hardly can be attributed to poor technique.

To illustrate these conclusions the efficiencies of protein and fat deposition, calculated according to equations (11), (12) and (13), are given for lamb K_1 in Tables 10 and 11.

With data from only 3 sheep, there should, of course, be no great pretence of representativeness. None the less, there are several features of Tables 10 and 11 worthy of comment.

Table 10

The efficiency of protein and fat deposition before 13 weeks of age of lamb K_1 *(MJ/MJ)*

	Protein			Fat		
Body mass	eq (11)	eq (12)	eq (13)	eq (11)	eq (12)	eq (13)
5	1,84	1,10	0,29	0,23	0,14	0,10
10	1,35	0,80	0,21	0,28	0,17	0,12
15	1,12	0,67	0,18	0,31	0,19	0,14
20	0,99	0,59	0,16	0,34	0,20	0,15
25	0,89	0,53	0,14	0,36	0,21	0,16

Table 11

The efficiency of protein and fat deposition after 13 weeks of age of lamb K_1 (MJ/MJ)

	Protein			Fat		
Body mass	eq (11)	eq (12)	eq (13)	eq (11)	eq (12)	eq (13)
25	1,68	0,99	0,08	0,31	0,18	0,17
30	1,35	0,80	0,07	0,34	0,20	0,18
45	0,84	0,49	0,04	0,41	0,24	0,22
60	0,60	0,35	0,03	0,46	0,27	0,25
75	0,46	0,27	0,02	0,51	0,30	0,28

1. Using a model similar to Orskov & MacDonald (1970) Hofmeyr (1972) reported partial efficiencies of 0,65 and 0,45 for protein and fat synthesis, respectively, for sheep of the Mutton Merino type. These estimates are included in the range of values derived from eq. (12) for protein, and serve as an upper boundary for the values derived from eq. (11) for fat.

2. The large number of efficiencies for protein larger than one from eq. (11), together with the more realistic estimates from eq. (12), indicate that so much heat production is associated with protein deposition as to render the assumption of constant heat production totally untenable. The situation is less extreme with fat.

3. It is of some interest to note that the efficiencies of protein deposition decrease with increase in body mass and those of fat deposition increase with body mass.

4. The gross efficiency of energy deposition can be obtained by adding, in Tables 10 and 11, the results from eq. (13) for protein and fat. The totals are given in Table 12.

The results in Table 12 are also of interest in their own right. The average gross efficiency of 36 percent for 5 and 10 kg is in excellent agreement with Rubner's value of around 35 percent for his index of gross efficiency during the doubling of birth weight of various animals (Needham, 1964). The rest of the table is also in very good agreement with Needham's (1964) observation that gross efficiency of growth is approximately constant over much of the growth cycle. In the light of the remarks on (14), this fact follows from the fact that the slopes between ln (cumulative heat production) and ln (cumulative DE or ME) are near to one, as follows from Tables 5 and 6.

It seems fair to conclude that an approach to a study of growth, efficiency and feed evaluation based on total energy retention (vide, for instance, Blaxter 1969) will result in useful approximation, but that extrapolation, beyond the experimental range, may result in large error if the conventional use is made of the partial efficiencies of protein and fat deposition.

Additional support for the single dimensional nature of the input-output system by which growth is described in this paper is summarized by Roux (1981). It follows that the dimension and curvilinearity of the system on the arithmetic scale invalidate any attempt to obtain answers on the cost of protein or fat deposition by ordinary multiple regression methods. The only con-

Table 12

The gross efficiency of energy deposition of lamb K_1 *(MJ/MJ)*

Before 13 weeks of age		After 13 weeks of age	
Body mass	Efficiency	Body mass	Efficiency
5	0,39	25	0,25
10	0,33	30	0,25
15	0,32	45	0,26
20	0,31	60	0,28
25	0,30	75	0,30

ceivable way by which constant costs of fat or protein synthesis can be obtained would be if the substitution of heat production by maintenance would change the dimension of the system. Since maintenance constitutes at least half of the heat production of homeotherms it seems very likely that such an interchange would leave the dimension of the relevant system unchanged. In a single dimensional system the proof, associated with (14), is applicable against the existence of constant partial efficiencies of protein and fat synthesis.

References

A.O.A.C., 1970. Official methods of analysis of the Association of Official Analytical Chemists, 11th ed. Ed. by W. Horwitz, Washington: Association of Official Analytical Chemists.

BLAXTER, K.L., 1969. The efficiency of energy transformation in ruminants. Publ. Eur. Assoc. Anim. Prod. No. 12 pp. 21-28.

BLAXTER, K.L. & BOYNE, A.W. 1970., A new method of expressing the nutritive value of feeds as sources of energy in the evaluation of feeds. Proc. 5th Symp. of Energy Metab. of Farm Animals, Vitznau, Switzerland. E.A.A.P. Publ. No. 13 pp. 9–16.

ELSLEY, F.W.H., McDONALD, I. & FOWLER, V.R., 1964. The effect of plane of nutrition on the carcasses of pigs and lambs when variations in fat content are excluded. *Anim. Prod.* 6, 141.

HOPKINS, J.W., 1966. Some considerations in multivariate allometry. *Biometrics* 22, 747.

HOFMEYR, H.S. 1972. Kwantifisering van faktore wat die Brutodoeltreffendheid van energie omsetting van voer by skape beïnvloed. D.Sc. (Agric.) Thesis, Fac. Agric., Univ. Pretoria.

KENDALL, M.G. & STUART, A. 1973. The advanced theory of Statistics. Volume 2. Charles Griffin, London.

KIELANOWSKI, J. 1965. Estimates of the energy cost of protein deposition in growing animals. *Proc. 3rd Symp. Energy Metab. Troon 1964. Publ. Eur. Assoc. Anim. Prod.* 11, 13.

KOTARBINSKA, M. & KIELANOWSKI, J. 1969. Energy balance studies with growing pigs by the comparative slaughter technique. *Proc. 4th Symp. Energy Metab. Publ. Eur. Assoc. Anim. Prod.* 12, 299.

MEISSNER, H.H. 1977. An evaluation of the Roux Mathematical Model for the functional description of growth. Ph. D. Thesis, Dept. Zool., University of Port Elizabeth.

MEISSNER, H.H. & BIELER, E.U. 1975. A note on the validity of using combinations of predictive equations for estimating body composition from tritialed water space. *S. Afr. J. Anim. Sci.* 5, 7.

MEISSNER, H.H., DE LA REY, GERHARDT, KATRINA, E. & VAN DER WESTHUIZEN, ELNA, 1976. Variasie in die liggaamsamestelling van die skaap. *Agroanimalia* 8, 69.

MEISSNER, H.H., ROUX, C.Z. & HOFMEYR, H.S. 1975. Voluntary feed intake, growth, body composition and efficiency in the sheep: Breed and sex differences. *Agroanimalia* 7, 105.

NEEDHAM, A.E. 1964. The Growth Process in Animals. Sir Isaac Pitman & Sons Ltd. London.

ORSKOV, E.R. & McDONALD, I. 1970. The utilization of dietary energy for maintenance and for fat and protein deposition in young growing sheep. *Proc. 5th Symp. Energy Metab. Vitznau, 1970. Publ. Eur. Assoc. Anim. Prod.* 13, 121.

ROUX, C.Z. 1976. A model for the description and regulation of growth and production. *Agroanimalia* 8, 83.

ROUX, C.Z. 1981. Animal growth in the context of time series and linear optimal control systems. *S. Afr. J. Anim. Sci.* 11, 57.

SUNDSTOL, F., EKERN, A. & HAUGEN, A.E. 1974. Description of a respiration unit for sheep, goats, calves and pigs. *Proc. 6th Symp. on Energy Metab. of Farm Animals. Hohenhein, B.R.D. E.A.A.P. Publ. No. 14,* pp. 249–251.

THORBEK, GRETE & NEERGAARD, LISE, 1970. Construction and function of an open circuit respiration plant for cattle. *Proc. 5th Symp. on Energy Metab. of Farm Animals, Vitznau, Switzerland, E.A.A.P. Publ. No. 13,* pp. 243–246.

TULLOH, N.N. 1963. The carcase compositions of sheep, cattle and pigs as functions of body weight. In Carcase Composition and appraisal of Meat Animals Ed. by D.E. Tribe. C.S.I.R.O., Melbourne, Australia.