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THE INFLUENCE OF DIETARY ENERGY ON A MATHEMATICAL MODEL FOR GROWTH, BODY COMPOSITION AND FEED UTILIZATION OF PIGS

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(Sleutelwoorde: *Dieetenergie, wiskundige model, groei, liggaamsamestelling, voerverbruik, varke)*

OPSOMMING: DIE INVLOED VAN DIEETENERGIE OP 'N WISKUNDIGE MODEL VIR GROEI, LIGGAAMSAMESTELLING EN VOERVERBRUIK BY VARKE

'n Wiskundige model tesame met data-analises is aangepas om die effek van variasie in energiekonsentrasie van die dieet, wat verkry is deur die byvoeging van verskillende proporsies saagsels, op die groeiende vark te bepaal. Energiekonsentrasie het die autoregressie-koëffisiënt van ln (kumulatiewe voerinname) en die helling van die loglineêre verwantskap tussen liggaamsvet en kumulatiewe voerinname (ME), beïnvloed. In kontras hiermee het die hellings van die loglineêre verwantskap tussen liggaamsmassa, kumulatiewe hitteproduksie, proteïen- en totale liggaamsenergie met kumulatiewe ME nie met energiekonsentrasie gevarieer nie, hoewel alle afsnitte met energiekonsentrasie varieer. Die betekenis van hierdie patroon van groeiresponsies word geïnterpreteer in terme van die meganismes wat groei beheer en die analises is op sodanige wyse gedoen dat dit interpolasie toelaat na saagselvlakke wat nie in die eksperiment ingesluit is nie.

SUMMARY:

A mathematical model together with data analyses were adapted to describe the effect of variation in dietary energy concentration, achieved by the inclusion of different levels of sawdust, on the growing pig. It was found that the autoregression coefficient of ln (cumulative feed intake) and the slope of the log-linear relationship between body fat and cumulative feed intake (ME) are influenced by energy concentration. In contrast, the slopes of the log-linear relationship of body mass, cumulative heat production, protein and total body energy with cumulative ME do not vary with energy concentration, although all intercepts are again found to vary. The significance of this pattern of growth responses is interpreted in terms of mechanisms controlling growth, and the analytic procedure allows interpolation to sawdust levels not included in the experiment.

The meat trade in South Africa requires pigs with a maximum amount of lean meat but with a restricted amount of fat, to be slaughtered at about 90 kg live mass as baconers, and 50 kg as porkers. Energy intake of the pig greatly determines the amount of fat stored in the pig body (Lewis & Hardy, 1970; Lodge, Cundy, Cooke & Lewis, 1972; Cooke, Lodge & Lewis, 1972). It is therefore important to relate energy intake by the pig to its growth pattern, body composition and to the efficiency with which ingested nutrients are utilized. *Ad libitum* intake of feed and a high dietary energy density have an advantageous effect on growth rate (Barber, Braude, Mitchell & Pitman, 1972; Cooke *et al.*, 1972). Nevertheless greater advantages may come from making energy intake depend on the end product required and on the efficiency with which the end product is produced.

Teague & Hanson (1954), Hochstetler, Hoefer, Pearson & Luecke (1959), Cole, Duckworth & Holmes (1967) and Baird, McCampbell & Allison (1970) showed that dietary fibre *per se* is not necessarily responsible for changes in gain and carcass characteristics, but rather the reduced energy content of high fibre diets. Baird, McCampbell & Allison (1975) studied the effects of both fibre and bulk of the diet and came to the conclusion that the pig eats to satisfy a nutrient or energy requirement. Bulk or fibre content is therefore likely to affect energy intake only by physically limiting volume of intake. Thus, it seems important that dietary energy should be diluted with a bulky, virtually inert, substance.

A substantial expenditure in labour and equipment is incurred when feed intake has to be restricted to ensure an acceptable carcass. A desirable alternative might be *ad libitum* feeding on bulky feed. Consequently it is important to quantify the effect of dietary energy density measured at an *ad libitum* intake level on the growth pattern, growth rate, body composition and nutrient utilization.

Furthermore, the generally accepted mass at slaughter of 50 kg for porkers and between 85 and 90 kg for baconers does not necessarily represent live masses at which optimal feed efficiency is attained. Consequently, it is desirable to evaluate the effect of energy intake on the performance of the growing pig over its entire growth period, with the aim of establishing the mass at which the pig must be slaughtered for optimum performance, both biologically and economically. Accordingly this investigation was planned to quantify the effects of dietary energy concentration and intake on pig growth and performance. This is the first of 2 papers on this topic, and will cover the development of a suitable model together with the analysis of data. The mathematical model used for description and prediction is an extension and adaptation of the work of Roux (1976).

Materials and methods

Experimental animals

A total of 75 Landrace X Large White crossbred castrates weaned at 3 weeks of age were used. Of these 12 pigs were slaughtered at 5 (3 pigs), 7 (3 pigs) and 8 (6 pigs) weeks of age before any nutritional treatment was imposed. The remaining 63 pigs were allotted to one of 6 nutritional treatments when 8 weeks old.

Piglets used in the experiment were castrated at an age of 2 weeks, weaned at 3 weeks and then reared as a litter group (excluding the females) to 5 weeks, whereafter they were individually reared in flat deck-type cages 1,6 x 1 metres in size, fitted with a self feeder and an automatic water nipple. Temperatures in the building were controlled to the extent that minimum temperatures never dropped below 20°C, while maximum temperatures seldom rose above 30°C, All pigs received the same creep feed (19,59% crude protein in the DM, and a metabolizable energy, ME, content of 15,28 MJ/kg DM) from a week prior to weaning to 7 weeks of age. Thereafter the experimental diets mixed with the creep feed on a 50:50 basis were fed until 8 weeks of age when the full experimental diets were introduced. Pigs were fed *ad libitum* at all stages. Feed intake and live mass were recorded on the same day at weekly intervals. Feed and water were not withdrawn before mass determinations.

Estimation of initial cumulative ME intake

The statistical analyses in this paper are based on the allometric relationships between cumulative ME intake, from the time of conception, and body mass or the components of body composition, as will be evident. Individual feed intake from conception up to 5 weeks of age had to be estimated. The total body protein and fat content of the 12 pigs slaughtered at 5, 7 and 8 weeks of age were determined according to the method described by Kemm & Ras (1976). From the data, the following regression equations for protein and fat content were calculated:

1. Protein: $\ln \text{mass (kg)} = 0{,}9053 \ln \text{protein (kg)} - 1{,}9282$

   $r^2 = 0{,}978 \quad \text{C.V.} = 1{,}88\%$

2. Fat : $\ln \text{mass (kg)} = 0{,}6579 \ln \text{fat (kg)} - 2{,}4717$

   $r^2 = 0{,}856 \quad \text{C.V.} = 4{,}89\%$

The above equations were then used to compute body protein and fat content at an age of 5 weeks for each pig to be used in the experiment. From these figures cumulative ME intakes from conception to an age of 5 weeks were calculated for each pig by using the conversion factors calculated by Thorbek (1970) for protein and fat synthesis. According to Thorbek the amount of ME required for protein synthesis is 49,8 MJ/kg protein synthesized and for fat the requirement is 51,9 MJ/kg. To this a maintenance allowance should be added.

The values for ME intake from conception to 5 weeks of age, based on the mass of the pig at 5 weeks, could therefore be added to the measured amount of feed (ME) of each experimental animal. This procedure was more acceptable than that of nonlinear estimation for initial feed intake in equation (1), as the nonlinear procedure gave grossly deviant estimates for some pigs. For the rest of the pigs the estimates of initial feed intake from both procedures showed good agreement.

Experimental treatments

The composition of each of the 6 diets fed from 8 weeks onwards is set out in Table 1. Diets 1 to 5 were compounded to contain 20% protein, equal in protein quality and origin and known to be in excess of the requirements for optimum production. A dilution of the dietary energy content of the diets was achieved by replacement of maize starch by equal amounts of pine wood sawdust. Diet 6 served as a control diet representing the type of growth diet presently used in South Africa.

Allotment of the pigs to the respective dietary treatments and the age at which they were slaughtered is set out in Table 2.

Slaughter procedure

Pigs on any one treatment were slaughtered one at a time at 2 week intervals from an age of 9 weeks up to 29 or 31 weeks when the last pig in a treatment was slaughtered.

Each pig was slaughtered at a predetermined age immediately after its mass was determined (water and food not being withheld beforehand). After electrical stunning each pig was suspended from the hind legs over a

Table 1

Experimental diets

Diet No.	1	2	3	4	5	6
Dietary component						
Yellow maize meal, kg	34	34	34	34	34	71
Fish meal, kg	26	26	26	26	26	12
Maize starch, kg	40	32	24	16	8	–
Pine wood sawdust, kg	–	8	16	24	32	–
Lucerne meal, kg	–	–	–	–	–	10
Wheaten bran, kg	–	–	–	–	–	5
Bone meal, kg	–	–	–	–	–	1
Salt, kg	0,5	0,5	0,5	0,5	0,5	1
Na_2HPO_4, kg	0,3	0,3	0,3	0,3	0,3	–
Material & Vitamin mixture, **	+	+	+	+	+	+
*Dietary composition**						
Crude protein content, %	23,8	23,6	23,2	23,4	23,2	19,2
Crude fibre content, %	1,5	7,3	12,3	17,7	22,7	5,6
ME content, MJ/kg DM ***	16,97	15,57	13,97	12,87	11,49	14,85

* Determined on a DM basis according to AOAC procedures.

** A commercial mixture was added according to the manufacturers prescription.

*** Determined in a metabolism trial with 6 pigs per diet.

Table 2

Age and live mass at slaughter of the pigs allotted to the various nutritional treatments

Treatment No.											
1		2		3		4		5		6	
Age, days	Mass, kg	Age, days	Mass, kg	Age, days	Mass, kg	Age, days	Mass, kg	Age, days	Mass, kg	Age, days	Mass, kg
78	27,25	78	25,25	77	23,25	77	19,50	77	22,00	76	26,75
90	33,50	90	31,75	90	31,50	90	25,25	90	23,95	90	36,50
105	42,50	105	45,50	105	36,50	104	31,50	106	24,75	106	44,25
118	48,25	119	54,25	119	43,00	119	46,25	119	35,75	119	62,50
122	44,75	–		–	–	–	–	–	–	–	–
135	70,50	136	64,50	132	57,75	132	51,25	132	36,75	132	63,00
147	82,75	146	75,25	148	71,50	148	63,50	148	50,25	146	80,75
162	78,25	–	–	161	79,50	–	–	162	52,25	161	84,50
174	79,50	175	80,00	174	87,00	175	75,00	175	60,25	174	84,00
188	108,25	191	111,50	188	90,50	188	85,00	192	67,75	188	103,25
204	121,00	202	118,50	207	106,25	207	103,25	202	76,50	202	106,50
–	–	–	–	216	109,00	217	83,00	216	90,50	216	119,00

plastic bin, its throat cut, and all the resulting blood collected in the bin. After removal of the gut and head, the carcasses were split medially down the back. The right side of each carcass was kept for carcass quality evaluation.

After measuring the mass of the left side, minus front and hind trotters, it was cut up into chunks and stored in air tight plastic bags in a deep freeze for chemical analyses. The head, trotters, blood and emptied gut were also stored in a deep freeze after mass determination for checmical analyses. The methods employed in grinding, sampling and chemically analyzing the carcass and offal components are described by Kemm & Ras (1976).

Statistical methods

(a) *Estimation and tests in the feed domain*

In regression analysis the x or independent variables should be measured virtually without error. Relative measurement error can often be expected to be least in the measurement of feed intake and, since all body energy processes are dependent on it, cumulative feed intake is also the variable with the largest difference between the smallest and largest observations. Hence, for ordinary regression equations it is, in the present circumstances, often an optimal procedure to use ln (cumulative feed intake) as x or independent variable. The logarithms of body mass, total energy, body protein, body fat and cumulative heat production are then treated as y or dependent variables. Any other relationship such as, say, body protein versus body mass can then be obtained by algebraic substitution. Even in cases where the other variables are measured accurately enough to be used as independent variables, this procedure is still efficient enough for most applications. Algebraic substitution in relationships with ln (cumulative feed intake) is equivalent to the use of instrumental variables in regression, and in the situation where, say, ln (body mass) is the proposed new independent variable, the relative estimation efficiency of the regression coefficient would be equal to the square of the correlation coefficient between ln (body mass) and (cumulative feed intake), vide Kendall & Stuart (1973, pp. 414, 435).

The model for the data from the slaughtered pigs is

$$y = a + bx + e, \qquad (1)$$

where x is ln (cumulative feed intake) and y is equal to the logarithms of the other variables of interest, at the point of slaughter. The usual tests and procedures are then assumed to apply.

(b) *Estimation and tests in the time domain*

In the time domain possible models follow from Roux (1976). For the data at the points of slaughter the model will be

$$y(t) = \alpha + \beta\rho^t + e(t), \qquad (2)$$

where α is asimptotic or adult value. Here each datum represents a different individual, so that the errors are independent. Equation (2) is in the time domain the equivalent of (1) in the feed domain.

From the theory of Roux (1976) ρ is an important parameter, associated with the partitioning of energy for protein and fat synthesis and for heat production. Hence its efficient estimation is of the utmost importance. When (2) was used for the estimation of ρ, it did not show a pattern against percentage sawdust in accordance with the pattern for the partitioning of energy, as indicated by the slopes of eq. (1). Hence it was decided to use the autoregressive model for estimation purposes,

$$y(t) - \alpha = \rho\,(y(t-1) - \alpha) + \varepsilon(t)$$

or

$$y(t) = \rho\, y(t-1) + \alpha\,(1 - \rho) + \varepsilon(t). \qquad (3)$$

For the application of equation (3) the cumulative feed intakes from 5 pigs from each treatment were used, with each pig having 10 or more weekly feed intakes.

The process represented by equation (3) is also known as a Markov process in the literature on time series, and its solution is, for

$$|\rho| < 1$$

$$y(t) = \alpha + \rho^t(y(0) - \alpha) + \sum_{j=0}^{t-1} \rho^j \varepsilon(t-j) \qquad (4)$$

with

$$\alpha + \rho^t(y(0) - \alpha) + \rho^t\beta \qquad (5)$$

(say) the so-called particular solution of the Markov process. In the literature on the estimation of ρ it is assumed that the process has been going on for such a long time that the particular solution is equal to α. However, in growth studies this is manifestly not the case. Hence, it follows that in Roux's (1976) equation (54) the denominator can be large in relation to the numerator, as it can be shown to be proportional to β^2. As the means of estimates of the ρ –s showed no trend with length of record it seemed safe to conclude that the usual bias in estimates of ρ with particular solution equal to α (instead of (5)) is, in the present situation, indeed negligible.

(c) *Notation*

Let

z_1 = cumulative feed intake

z_2 = cumulative heat production (6)

z_3 = body protein

z_4 = body fat

z_5 = body mass

z_6 = total body energy

Let also

$$x_i = \ln(z_i) \qquad (7)$$

for $i = 1, 2, \ldots, 6$, and note that

$$z_i = \exp(x_i).$$

Statistical analyses

1. *Estimates and tests in the time domain*

The applicability of Roux's (1976) theory depends on linear relationships. To this end, logarithmic relationships are used, and besides linear relationships between the different characteristics, linearity should also be revealed by autoregressive plots of $x_i(t)$ versus $x_i(t-1)$, where $x_i(t)$ is the value of the i-th characteristic at week t and $x_i(t-1)$ is the value of the same at week $(t-1)$. Plots of this kind are given in Figures 1 and 2, of the 2 individual pigs with the longest records from Treatments 1 and 5, respectively. Note the breaks in the lines associated with ln (cumulative ME, MJ) at week 11 on the X-axis and week 12 on the Y-axis indicated by the arrows in the figures. In Figure 2 the change to the diet containing 32% sawdust is indicated by a single deviant point. It would seem, therefore, that perhaps some sort of physiological change was associated with 11 weeks of age in the experimental animals. The existence of a similar breakpoint at approximately 11 weeks of age was confirmed for additional animals on all treatments. For a discussion on the significance and physiological relationships of these breakpoints Scholtz & Roux (1980) can be consulted.

Breakpoints at 11 weeks of age are also evident from Figures 3 and 4 where the plots of the animals of Figures 1 and 2 are shown for ln (body mass, kg) against ln (cumulative ME, MJ), with all measurements taken with weekly intervals. In the light of the results from plots like Figures 1–4 it was decided to analyse all data from the 11th week onwards.

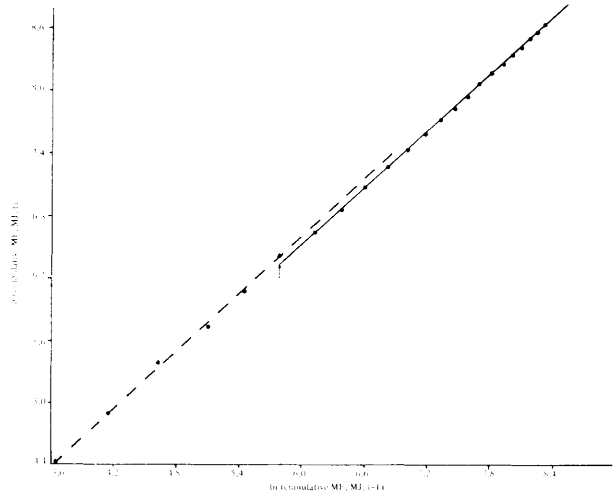

Fig. 1; *Autoregressive plot for a single pig from Treatment 1. The breakpoint is indicated by an arrow*

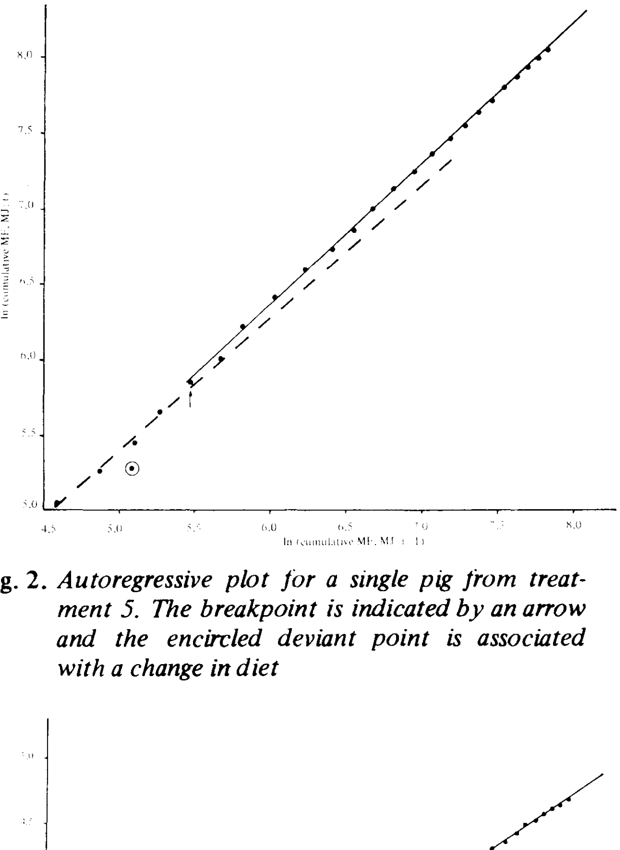

Fig. 2. *Autoregressive plot for a single pig from treatment 5. The breakpoint is indicated by an arrow and the encircled deviant point is associated with a change in diet*

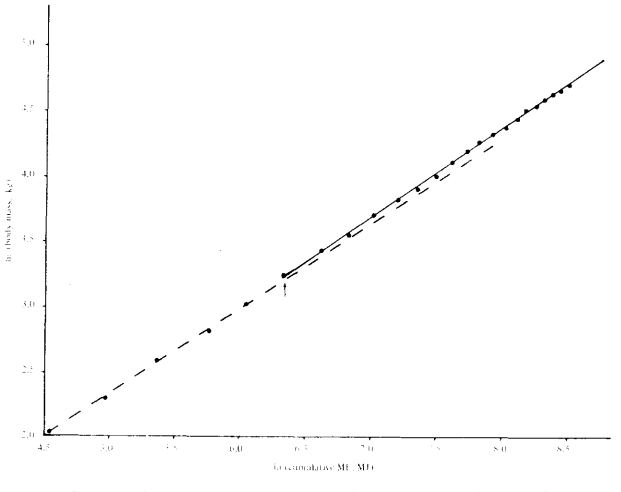

Fig. 3. *Plot of ln (body mass, kg) against ln (cumulative ME, MJ) for an individual from Treatment 1. The breakpoint is indicated by an arrow*

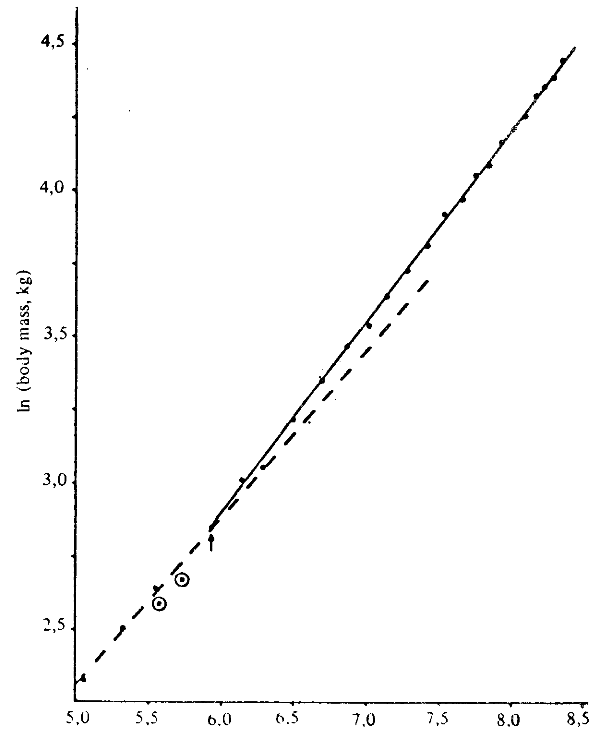

Fig. 4. *Plot of ln (body mass, kg) against ln (cumulative ME, MJ) for an individual from Treatment 5. The breakpoint is indicated by an arrow and the encircled deviant points are associated with a change in diet*

(a) *The estimation of the autoregression coefficient*

Estimation of ρ according to (2) produced standard errors much larger than those obtained according to (3), as the averages of 5 animals per treatment with the variances calculated from the between animals, within treatment, line in the analysis of variance. The estimates of ρ, , $\bar{\rho}$, obtained in this fashion are given in Table 3.

The values of $\bar{\rho}$ for treatments 1 and 2 and also for treatments 4 and 5 are very near to each other, with a significant difference (at the one per cent level) between 2 and 4. The estimates labelled $\hat{\rho}$ in Table 3 were obtained by averaging treatments 1 and 2 and 4 and 5. The average of these 2 means agrees well with the $\bar{\rho}$ of 3. Hence the procedure to obtain estimates of ρ for any sawdust proportion would be to use

$$\begin{array}{ll} \text{estimate of } \rho & \textit{sawdust proportion (p)} \\ 0{,}9098 & p \leqslant 0{,}08 \\ 0{,}9098 \leqslant \hat{\rho} \leqslant 0{,}9291 & 0{,}08 \leqslant p \leqslant 0{,}24 \\ 0{,}9292 & p \geqslant 0{,}24 \end{array} \qquad (8)$$

with linear interpolation according to ρ for $0{,}08 \leqslant p \leqslant 0{,}24$.

Table 3

Estimates for feed intake parameters of the autorepressive relationship

Sawdust proportion Treatment No.		0 1	0,08 2	0,16 3	0,24 4	0,32 5	– 6	s.e.
	Dimension							
$\bar{\rho}$	ln (wk^{-1})	0,9105	0,9090	0,9183	0,9290	0,9292	0,9091	0,0042
$\hat{\rho}$	ln (wk^{-1})	0,9098	0,9098	0,9194	0,9291	0,9291	–	0,0030
$\bar{\alpha}$	ln (MJ)	8,8893	8,8516	8,9576	9,0202	8,7987	8,9050	0,1091
$\bar{x}(0)$	ln (MJ)	6,4662	6,3302	6,2356	6,1253	5,9332	6,3502	0,0878
$\hat{x}(0)$	ln (MJ)	6,4723	6,3452	6,2181	6,0910	5,9639	–	0,0555
$\bar{\beta}$	ln (MJ)	2,4230	2,5214	2,7220	2,8949	2,8655	2,5548	0,1389
$\hat{\beta}$	ln (MJ)	2,4312	2,5583	2,6854	2,8125	2,9396	–	–
$\hat{c}$	wk^{-1}	0,0250	0,0250	0,0208	0,0179	0,0170	–	–

Grand mean, $\bar{\alpha}$ = 8,9035

s.e. = 0,0488

(b) *The estimation of α*

Equation (3) was used to estimate α for each of the 5 individuals (with the longest records) per treatment. A two-way analysis of variance revealed no significant differences between treatments or length of record. This is in contrast to the situation in ρ, where highly significant treatment effects were observed. The mean values for the α – s, $\bar{\alpha}$, are given in Table 3. However, from the nonsignificance of treatment effects in the analysis of variance and from a lack of relationship with proportion sawdust, the conclusion is that α is a constant for all the treatments under consideration, with the grand mean $\bar{\alpha}$ = 8,9035; s.e. = 0,0488.

(c) *The estimation of βc*

A plot of $\bar{x}_1(0)$ (time zero being 11 weeks) for the 5 animals in each treatment with the longest records, shows a linear relationship with proportion sawdust

$$\bar{x}_1(0) = a + bp + e, \tag{9}$$

(see table 3), from which the predicted values of $\bar{x}_1(0)$, $\hat{x}_1(0)$, can be calcualted. $\hat{\beta} = \bar{\alpha} - \hat{x}_1(0)$ is given for each treatment in Table 3. In the autoregressive form (equation (3)) $x_1(0)$ is often regarded as fixed or given, so that the variances of $\bar{\alpha}$ and $\hat{\beta}$ are assumed to be the same.

2. *Estimates and tests in the feed domain*

The loglinearity of the measures reflecting body composition is exhibited by Figures 5–7 for Treatment 1 and Figures 8–10 for Treatment 5, with these 2 treatments representing the extremes of 0 and 32% sawdust. Hence the model employed is the ordinary regression model

$$x_i(t) = a_i + b_i x_1(t) + e(t), \tag{10}$$

for 1 = 2, 3, ..., 6, the traits being indicated by numerals according to (6).

(a) *Slopes*

Covariance analyses revealed significant differences between the slopes for different treatments only in the case of fat (see Table 4). The slopes with nonsignificant treatment effects are given in Table 5.

Inspection of Table 4 shows that b_4 is likely to be the same for the first 2 treatments. For the rest of the treatments b_4 seems to be loglinearly related to sawdust proportion.

Table 4

Slopes for regression with ln (cumulative ME-intake) as independent variable and ln (fat) as dependent variable

Sawdust proportion Treatment No.	0 1	0,08 2	0,16 3	0,24 4	0,32 5	– 6
b_4	1,2141	1,2197	1,3047	1,3476	1,3918	1,2291
s.e.	0,0403	0,0424	0,0357	0,0361	0,0374	0,0393
$\hat{b}_4$	1,2174	1,2174	1,3008	1,3523	1,3900	–
s.e.	0,0241	0,0241	0,0241	0,0241	0,0241	–

Table 5

Slopes with ln (cumulative ME-intake) as independent variable

	ln (cumulative heat production)	ln (protein)	ln(body mass)	ln (total body energy)
b_i	0,9703	0,5894	0,6787	1,0515
s.e.	0,0060	0,0131	0,0095	0,0115

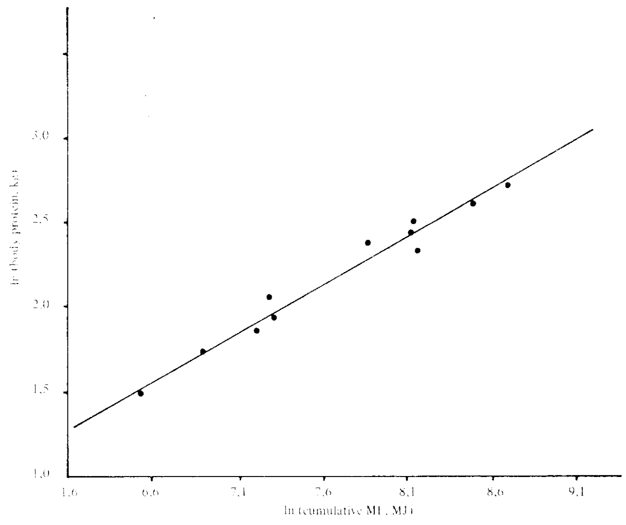

Fig. 5. *Plot of ln (body protein, kg) against ln (cumulative ME, MJ) for the slaughterpoints of Treatment 1*

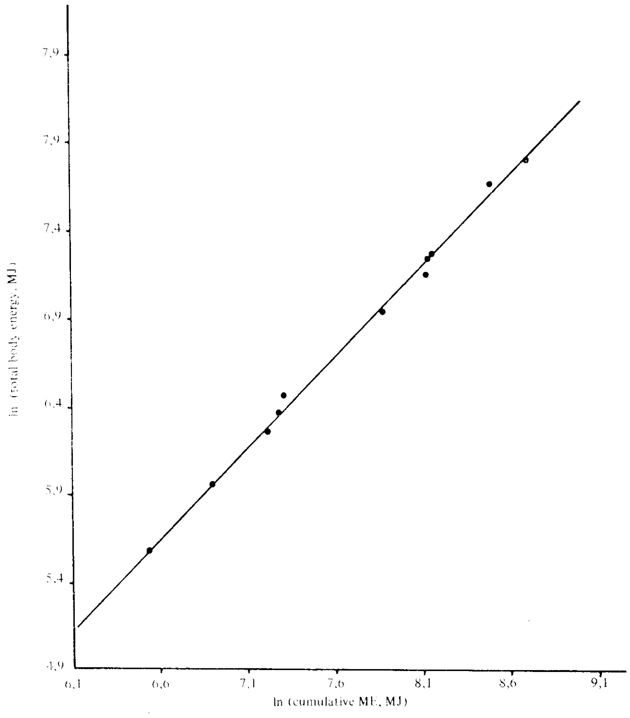

Fig. 7. *Plot of ln (total body energy, MJ) against ln cumulative ME, MJ) for the slaughterpoints of Treatment 1*

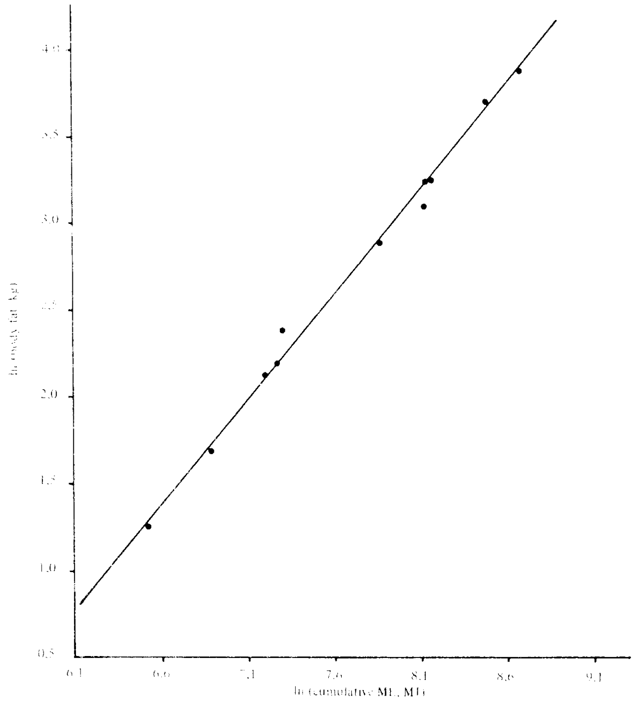

Fig. 6. *Plot of ln (body fat, kg) against ln (cumulative ME, MJ) for the slaughterpoints of Treatment 1*

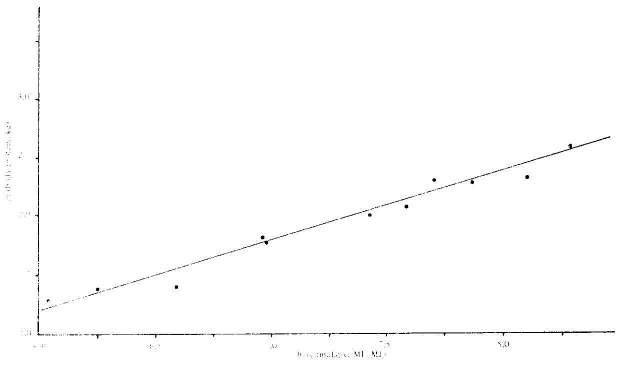

Fig. 8. *Plot of ln (body protein, kg) against ln (cumulative ME, MJ) for the slaughterpoints of Treatment 5*

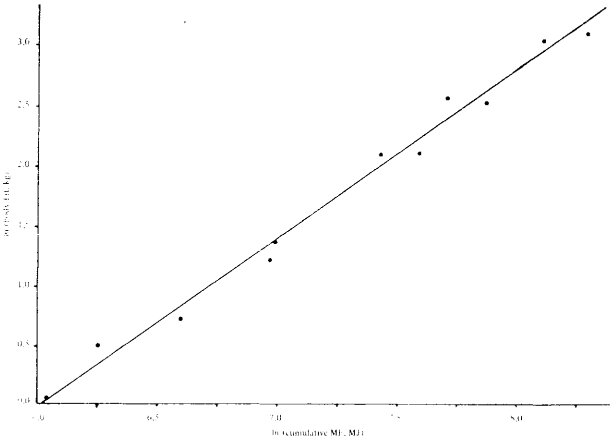

Fig. 9. *Plot of ln (body fat, kg) against ln (cumulative ME, MJ) for the slaughterpoints of Treatment 5*

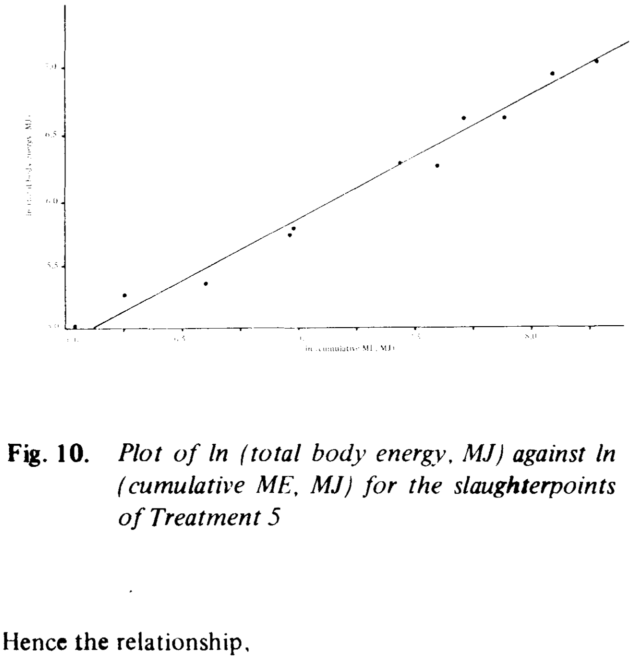

Fig. 10. *Plot of ln (total body energy, MJ) against ln (cumulative ME, MJ) for the slaughterpoints of Treatment 5*

Hence the relationship,

$$\hat{b}_4 = 1{,}5502p^{0{,}0957}, \qquad (11)$$

for $p \geqslant 0{,}08$ was obtained by ordinary linear regression. The average standard errors of the estimates obtained by (11) are in Table 4.

(b) *Intercepts*

In all cases, except for protein, significant difference in intercepts resulted from the covariance analyses. These are given in Table 6, on the first line for each trait under consideration.

To obtain the relationship of the intercepts with the proportion sawdust the easiest way is to consider the relationships of the $\bar{x}_i$ – s (i = 1, 2, ..., (6) with proportion sawdust, p, where the $\bar{x}_i$–s are as defined in (6) and (7).

The pattern suggested by the data is most clearly displayed by body mass. Here $\bar{x}_5$ remained nearly constant from zero to 16% sawdust, with a rather sharp, approximately linear, decline from 16 to 32% sawdust. This pattern is the result of the homeostatic properties of the animals, reflecting the greater intake in mass-units, to offset the lower energy concentration of the feed up to approximately 16% sawdust. From 16% sawdust onwards the pigs probably reached the limit of their capacity to ingest enough food to offset the greater bulk of the rations.

Apart from body fat, this sort of pattern was more or less displayed by all the traits under consideration, with sometimes a small decline on the values of $\bar{x}_i$, also for the first 3 sawdust percentages. The relationships of the $\bar{x}_i$ with proportion sawdust are displayed in Table 7, and the intercepts calculated by the relationship,

$$\hat{a}_i = \hat{x}_i - b_i \bar{x}_1, \qquad (12)$$

for i = 2, 3, 4, 5, 6, are displayed in Table 6, where $\hat{x}_i$ is the estimated value of $\bar{x}_i$, from its linear relationship with proportion sawdust. The variance of $\hat{a}_i$ is

$$\mathrm{var}\,(\hat{a}_i) = \mathrm{var}\,(\hat{x}_i) + \bar{x}_1{}^2\,\mathrm{var}\,(b_i).$$

In the situation where $\hat{x}_i$ is from one of the observed sawdust proportions, its variance is $\frac{\sigma^2}{n_1 + n_2 + n_3}$ if the first 3 treatments resulted in approximately constant estimates, and its average variance is $\frac{2\,\sigma^2}{n_1 + n_2 + n_3}$ in the situation where a regression line is used.

$\hat{\sigma}^2$ is estimated from the ordinary covariance analyses against ln (cumulative ME), and is given in Table 7.

In the case of fat, where a single regression line against the square of proportion sawdust is used

$$\mathrm{var}\,(\hat{x}_4) = 2\,\hat{\sigma}^2 \Big/ \sum_{i=1}^{5} n_i,$$

with $\hat{\sigma}^2$ again obtainable from Table 7.

Var (b_i) is obtainable from Tables 4 and 5.

If one wishes to estimate the variance for $\hat{x}_i$ for the mean of n_x new observations, $\hat{\sigma}^2/n_x$ should be added, as usual.

Table 6

Intercepts with ln (cumulative feed intake) as independent variable

Sawdust proportion Treatment number	0 1	0,08 2	0,16 3	0,24 4	0,32 5	– 6	Mean s.e.
ln (cumulative heat production)	–0,2924	–0,2696	–0,2272	–0,1987	–0,1196	–0,2794	0,0466
treatments 1, 2, 3	–0,2810	–0,2631	–0,2451	–	–	–	0,0466
treatments 3, 4, 5	–	–	–0,2357	–0,1819	–0,1281	–	0,0456
ln (protein)	–2,2984	–2,2984	–2,2984	–2,2984	–2,2984	–2,2984	0,0987
treatments 1, 2, 3	–2,2825	–2,2825	–2,2825	–	–	–	0,0999
treatments 3, 4, 5	–	–	–2,2690	–2,3020	–2,3351	–	0,0986
ln (body mass)	–1,0583	–1,0445	–1,0512	–1,0883	–1,1347	–1,0469	0,0736
treatments 1, 2 3	–1,0512	–1,0512	–1,0512	–	–	–	0,0729
treatments 3, 4, 5	–	–	–1,0495	–1,0912	–1,1329	–	0,0719
ln (total body energy)	–1,2985	–1,3339	–1,4043	–1,4591	–1,6312	–1,3199	0,0892
treatments ,1, 2, 3	–1,2773	–1,3460	–1,4147	–	–	–	0,0891
treatments 3, 4, 5	–	–	–1,3859	–1,5027	–1,6194	–	0,0871
ln (body fat)	–6,5218	–6,2667	–7,3736	–7,7467	–8,3345	–6,6621	0,3205
treatments 1, 2, 3	–6,5228	–6,5803	–7,3853	–	–	–	0,1663
treatments 3, 4, 5	–	–	–7,3680	–7,8298	–8,2902	–	0,1663

Note:

1. The units of measurement for body mass, protein and fat are ln (kg), and those of heat production, feed intake and body energy are ln (MJ)
2. The first line for each trait is from ordinary covariance analysis.
3. The second and third lines for each trait are from Table 7, by procedures indicated in the text.

Procedures exist by which the lines for the first 3 points (sawdust inclusion rates) and the lines for the last 3 points can be made to intersect at 16% sawdust. It was, however, decided that the embarassment of 2 estimates of intercepts at 15% sawdust is a lesser evil than the spurious impression of accuracy from a single estimate.

It is of some interest to note that, in Table 6, no great gain in accuracy (as measured by the standard errors) resulted, except in the situation of body fat. The estimates from (12) are in good agreement with those from ordinary covariance analysis, if the standard errors are taken into account. However, although the gains in accuracy are slight, the estimates of slopes and intercepts from the equation, $\hat{x} = \hat{a} + \hat{b}(p - \bar{p})$, with $\hat{a}$ and $\hat{b}$ given in Table 7, allow interpolation to proportions of sawdust not included in the experiment. Note that for the first 3 treatments $\bar{p} = 0,08$ and for the second 3 $\bar{p} = 0,24$. For fat the regression relationship is $\hat{x} = \hat{a} + \hat{b}(p^2 - \bar{p}^2)$.

Table 7

Regression equations for the estimation of mean values $(\bar{x}_i)$

		Treatments		
		1, 2, 3	3, 4, 5	$\hat{\sigma}$
ln (cumulative heat production) (MJ)	Slope	0,2244	−1,2606	0,0344
	S.e.	0,0515	0,0240	
	Intercept	7,0963	7,0100	
	S.e.	0,0062	0,0061	
ln (protein) (kg)	Slope	0	−1,5875	0,0760
	S.e.	–	0,0476	
	Intercept	2,1879	2,0666	
	S.e.	0,0137	0,0134	
ln (body mass) (kg)	Slope	0	−1,8738	0,0538
	S.e.		0,0310	
	Intercept	4,0965	3,9000	
	S.e.	0,0097	0,0095	
ln (total body energy) (kg)	Slope	−0,8588	−3,544	0,0651
	S.e.	0,0515	0,0273	
	Intercept	6,6293	6,2935	
	S.e.	0,0117	0,0115	
ln (body fat) (kg)	Slope	−8,9834	−8,9834	0,0882
	S.e.	0,0226	0,0226	
	Intercept	2,3659	2,3659	
	S.e.	0,0125	0,0125	
ln (cumulative ME) (MJ)	Slope	0	1,9925	–
		–		
	Intercept	7,5847	7,4120	

3. *Relationships with time of the traits measured by slaughter*

To obtain the expected (mean) values, $E(x_i(t))$, in (4) for the slaughter traits and body mass use is made of

$$b_i = \frac{\beta i}{\beta_1}$$

and

$$\alpha_i = a_i + b_i \alpha_1,$$

vide Roux (1976), for i = 2, 3, 4, 5, 6.

Discussion

It follows from theory developed by Roux (1976) that growth and rate of feed intake are proportional to $\gamma = -\ln\rho = c(1 + b_2^2 + b_3^2 + b_4^2)$, with c constant with dimension the inverse of time. Hence it seems that γ can only be influenced by a change in the slopes of (10), i = 2, 3, 4. This is in agreement with the change of b_4 (the slope of fat against cumulative ME) with proportion sawdust.

However, contrary to expectation b_4 increases with percentage sawdust, from which it should follow that ρ decreases with proportion sawdust. The contrary is observed, and a contradiction results, which can be removed only by assuming a change in c in the equation for γ. The values of c obtained by the substitution of estimates are given in Table 3.

This result is in agreement with the results of Meissner (1977) on ruminants, where roughages show an increase in b_4 in relation to concentrates. Hence it seems that c must be directly related to energy concentration of feeds. The finding of Meissner (1977) and Meissner, Hofmeyr & Roux (1977) that a direct reduction of intake, of the same feed, results in reduction of b_4 and the constancy of c, merely serves to strengthen this conclusion. The 2 situations portray, however, a basic dissimilarity of operative mechanisms between reduction of energy intake while *ad libitum* feed intake is maintained and reduced energy intake by allowing less of a given diet.

The theory developed by Roux (1976) allows the approach of deciding on, say, a desired fat percentage at a given mass, and by algebraic manipulation then to choose a b_4 that will give the desired end result, if b_2 and b_3 remain approximately constant. The choice of a reduced b_4 will generally lead to a reduced γ **for** feed intake and consequently a reduced growth rate. The constancy of b_2 and b_3 observed under treatment differ-

Table 8

The percentage values of the latent roots of the covariance matrix of the logarithms of cumulative metabolisable energy intake, body protein, body fat and cumulative heat production

Treatment No.	No. of animals	Largest root	Second root	Third root	Smallest root
1	11	99,5	0,3	0,2	0,0
2	9	99,4	0,5	0,1	0,0
3	11	99,6	0,3	0,1	0,0
4	10	99,6	0,2	0,2	0,0
5	11	99,3	0,5	0,2	0,0
6	11	99,4	0,4	0,2	0,0

Table 9

Regression coefficients and their standard errors

Pig No.	Treatment	d.f.	h_1	s.e.	h_2	s.e.
311	1	14	1,094**	0,127	−0,162	0,114
160	1	18	0,608*	0,225	0,274	0,204
112	2	12	1,048**	0,193	−0,115	0,176
314	2	14	0,435*	0,157	0,418*	0,144
312	3	16	1,056**	0,221	−0,129	0,201
109	3	14	1,382**	0,274	−0,423	0,253
355	4	16	0,995**	0,243	−0,069	0,224
113	4	14	0,571*	0,259	0,353	0,244
161	5	16	0,888**	0,249	0,046	0,234
310	5	14	0,661*	0,243	0,234	0,223
315	6	14	0,958**	0,251	−0,047	0,226
163	6	16	0,706*	0,243	0,191	0,223

* Significant at the 5% level

** Significant at the 1% level

ences in this experiment lends strength to the logic underlying this procedure, viz. that fat is the only body component under effective experimental control. In terms of fat percentage there is no reason to expect any difference between the reduced ration and reduced energy intake (at *ad libitum*) procedures.

Even though a line may still go through a fixed point, a change in slope will necessarily result in a change in intercept. This is part of the explanation of the change in intercept of ln (fat) versus ln (cumulative ME). The change of intercepts of protein and heat production must be accounted for in a wholly different manner. The mechanism enforcing a change in intercept is suggested by the equation reflecting the conservation of energy (the equation following on (55) in Roux (1976)) viz.

$$dz_1 = \sum_{i=2} \left(\frac{b_i}{b_2^2 + b_3^2 + b_4^2}\right) z_1 \frac{dz_i}{z_i}. \qquad (13)$$

Say that the changes induced by sawdust in the b-s have taken place, and that the intake of an animal (dz_1) is still not enough to balance the 2 sides of (13). Then growth would cease temporarily until the changes in the z_i relative to z_1 are such that the equilibrium is portrayed by (13). Maintenance of the equilibrium (13) will then, together with the other control equations of (Roux (1976), result in the regular growth paths of the animals on the different treatments. This was observed in Figures 2 and 4 from the 11th week onwards, after the initial period of adaptation in weeks 9 and 10 to the different sawdust diets.

The resumption of growth on a regular path can be portrayed by initial conditions (the values at week 11) in the solution to differential equations, which will be reflected by changes in the intercepts of (10), as is given in Roux (1976), equations (14) to (16). The linearity of the growth paths relative to ln (cumulative ME) together with (13), therefore, supply the explanation for the significant changes in intercept given in Table 6, although no change in slope occurred and the pigs from the different treatments started off from approximately the same average point before the treatments began.

In Roux (1976) a heuristic argument is given in support of the correspondence between the differential equations describing growth and feed intake and Hopkins' (1966) definition of multivariate allometry. Hopkins generalised the two-dimensional allometric relationships to the multivariate case by requiring a covariance matrix of rank one after the effect of measurement error or individual variation is removed. The rigorous derivation of difference equations describing growth and feed intake from a covariance matrix of rank one will be the subject of a theoretical paper by Roux.

The results of a principal components analysis are displayed in Table 8. The results seem consonant with the idea of a single dominating root, with the rest resulting from the combined effects of measurement error and individual variation. Hence the theory used in this paper is applicable. A further test would be to establish the adequacy of a first order autoregressive model. Hence h_2 is tested for significance in a model.

$$x_1(t) = g + h_1 x_1(t-1) + h_2 x_1(t-2) + \varepsilon(t),$$

where $x_1(t)$ is ln (cumulative ME intake) at time t. The results are given in Table 9 for pigs slaughtered near the end of the experiment. Since 12 pigs are involved, a single significant h_2 is likely to occur. Hence the conclusion that the data are consonant to a first order or Markov process.

All the statistics (or biological parameters) of usual interest, such as feed intake (MJ/day), growth in body mass or energy, etc. can be obtained from the estimates of the statistical parameters of this paper, by the usual mathematical procedures of algebraic substitution or differentiation, as the case may be. The statistics and interpretation of immediate biological interest have been published by Kemm (1980).

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