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THE DESCRIPTION OF GROWTH IN BEEF BULLS AND INTERPRETATION OF GENOTYPIC DIFFERENCES ON TWO DIETARY TREATMENTS

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(Sleutelwoorde: *Groei, vleisbeesbulle, genotipiese verskille, kragvoer, ruvoer)*

OPSOMMING: 'N BESKRYWING VAN GROEI BY VLEISBEESBULLE EN DIE INTERPRETASIE VAN GENOTIPIESE VERSKILLE OP TWEE DIËTE

Groei by vleisbeesbulle is bestudeer aan die hand van drie genotipes, naamlik die Afrikaner, Hereford en Simmentaler. Die ondersoek het gestrek vanaf geboorte tot sowat 80-weke ouderdom. Die helfte van die bulletjies het 'n kragvoerdieet ontvang en die ander helfte 'n ruvoerdieet en metings van lewende massa, vrywillige voerinname en liggaamsamestelling met behulp van tritiumverdunning is onafgebroke geneem. Die skynbare verteerbaarheid van voerenergie (VE) by *ad lib.* inname is ook met tussenposes gemeet.

Genotipe en ouderdom het nie die VE% in die dieet beïnvloed nie, en die gemiddeld vir die kragvoerdieet was 68,4 ± 2,2% en vir die ruvoerdieet 60,0 ± 5,3%. Die groeiresultate is ontleed en geïnterpreteer relatief tot persentasies van volwasse massa om grootte-effekte uit te skakel. Die inname van die Afrikaner was laer as dié van die Hereford en Simmentaler op die kragvoerdieet en dieselfde of selfs hoër op die ruvoerdieet. Hierteenoor was groei op beide diëte laer, terwyl min verskille tussen die Hereford en Simmentaler te bespeur was. Gevolglik was doeltreffendheid in terme van sowel kg DM inname/kg toename in leë massa en MJME inname/MJ toename in leë liggaamsenergie swakker by die Afrikaner as die ander twee genotipes wat weer eens nie noemenswaardig verskil het nie. Ten opsigte van liggaamsamestelling was die Herefords die vetste gevolg deur die Afrikaner en die Simmentaler, terwyl die Simmentaler die meeste vetvrye weefsel en proteïen gehad het, gevolg deur die Afrikaner en Hereford. Die patroon van genotipe verskille op die twee diëte was dieselfde, maar die bulletjies was vetter op die kragvoerdieet en het gevolglik minder vetvrye weefsel en proteïen as op die ruvoerdieet gehad.

Aangesien doeltreffendheid soos hier gedefinieër, by die Hereford en Simmentaler bykans dieselfde was ongeag van groot verskille in liggaamssamestelling, is die gevolgtrekking gemaak dat sodanige verskille 'n relatief klein bydrae tot doeltreffendheid maak. Die grootste bron van variasie in doeltreffendheid moet gesoek word in die energieverlies vir die sisteem, dit wil sê, energie wat nie in die liggaam teruggehou word nie, soos geïllustreer deur die Afrikaner. Dit is langs hierdie weg dat seleksievordering vir doeltreffendheid by vleisbeeste ondersoek moet word.

SUMMARY:

Growth of beef bulls has been studied with the aid of the three genotypes, the Afrikaner, Hereford and Simmentaler. The study ranged from birth to about 80 weeks of age. Half of the bull calves were raised on a concentrate diet and the other half on a roughage diet. Measurements were continuously taken on live mass, voluntary intake and body composition using tritium dilution while intermittent measurements were made of apparent digestibility of feed energy (DE) at *ad lib.* intake.

Genotype and age did not influence dietary DE%, the average on the concentrate diet was 68,4 ± 2,2% and on the roughage diet 60,0 ± 5,3%. The growth results were analysed and interpreted relative to percentages of mature mass to account for differences in size. The intake of the Afrikaner on the concentrate diet was lower than that of the Hereford and Simmentaler and the same or even higher on the roughage diet. Growth on the other hand was less on both diets while that of the Hereford and Simmentaler were approximately the same Consequently, efficiency in terns of both kg DM intake/kg gain in empty body mass and MJ ME intake/MJ gain in empty body energy was poorer for the Afrikaner than the other two breeds which again were very similar. As regards body composition, the Herefords were the fattest followed by the Afrikaner and Simmentaler, while the Simmentaler had the highest content of lean tissue and protein followed by the Afrikaner and the Hereford. The pattern of genotypic differences on the two diets was the same, but the calves were fatter on the concentrate diet, or the animals on the roughage diet had more lean tissue and protein.

Since efficiency as defined here, was very similar for the Hereford and Simmentaler irrespective of large differences in body composition, it was concluded that such differences account for only a relatively minor portion of the variation in efficienty. The major portion is accounted for by the energy loss from the system, i.e. energy which is not retained in the animal body, as demonstrated by the Afrikaner. The latter avenue should be explored in selection for efficiency in beef cattle.

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The quantification of differences between genotypes has considerable bearing on studies of nutritional requirements and the construction of breeding and selection programs to increase productivity. In studies of this nature it is preferable to look at the entire or major part of the growth curve and to measure all aspects known to affect growth and efficiency (Meissner, 1977). This would present a number of comparable physiological phases, but in particular would allow comparison at the same "physiological age" (Brody, 1945).

Since the pioneering work of Haecker (1920) and Moulton, Trowbridge & Haigh (1922) researchers seem to have been reluctant to do experiments of such vast magnitude, but instead have concentrated their efforts to answering questions within a particular set of comparable circumstances. There is little doubt that the Haecker-type of study would also be valuable in current times.

In this paper the growth and the composition of growth of three genotypes, the Afrikaner, the Hereford and the Simmentaler on 2 dietary regimes are reported. An extended period of growth lasting 80 weeks and live masses up to 500 - 600 kg was considered. An attempt has also been made to interpret genotypic differences.

Materials and Methods

Experimental procedure

Bull calves of the Afrikaner, Hereford and Simmentaler breeds were obtained 48 hours following birth. They were raised on cows milk until 11 weeks of age whereafter they were *ad lib.* fed on a concentrate (C) or a roughage (R) diet until about 80 weeks of age. Continuous measurements were made of intake, live mass, body composition (tritium dilution) and intermittent measurements of digestibility of dietary energy.

Details of experiment

Allocation of calves to diets

Calves were alternatively allocated to the 2 diets i.e., in order that they were born. The numbers of each breed and their birth masses are shown in Table 1.

Treatment prior to weaning

The calves were hand reared on cow's milk until 11 weeks of age according to a schedule in which the allowance relative to metabolic mass declined progressively.

As supplement they received a creep feed consisting of 70% maize meal, 20% lucerne meal and 10% fish meal from the age of 2 weeks. At the age of 8 weeks 25% of the creep was replaced by either diet C or diet R and at the age of 10 weeks 50% of the creep was replaced. From 11 weeks onwards diet C or R became the sole source of energy intake.

Composition of diets

The ingredients used to compile diets C and R are shown in Table 2.

Diet C was fed in pellet form and diet R in milled form. Eragrostis hay which constituted the major part of diet R, was milled through a 13 mm sieve.

Method of feeding

The animals were fed individually. An amount of feed enough for 1 week was weighed out at the beginning of each week. The daily allowance was given in 3 to 4 portions to ensure that fresh feed was always at hand. Refusals were bulked at the end of every week and the dry matter (DM) percentage determined in order to obtain the amount of DM voluntarily consumed per week. Water was always available.

Table 1

Mean birth mass and numbers of calves allocated to the diets

Genotype	n	Diet C Birth mass (kg)	n	Diet R Birth mass (kg)	F-values for difference between		
					Diets	Genotypes	Interaction
Afrikaner	6	31,8 ± 2,48	7	32,9 ± 5,30			
Hereford	5	34,2 ± 1,92	5	34,0 ± 3,74	0,073	16,2***	0,278
Simmentaler	5	45,5 ± 9,05	6	43,2 ± 6,48			

*** p < 0,001

Table 2

The composition of diet C and R on an air-dry basis.

	Diet C (%)	Diet R (%)
Maize meal	42,9	8,0
Eragrostis bay	10,0	79,0
Sorghym meal	5,5	–
'Hominy' chop	6,3	–
Maize hay	16,9	–
Fish meal	–	8,0
Oil cake meal	6,0	4,0
Urea	1,3	–
Molasses	10,0	–
Calcium carbonate	1,0	–
Sodium chloride	1,0	1,0
Micro elements	0,05	–
Vitamin A	12 g/ton	–
*Micro elements & vitamins	–	1 kg/ton
* Commercial mixture was used		
	%	%
Calculated DE	70	60
Calculated CP	13,5	12,5
Calculated Ca	0,55	0,63
Calculated P	0,33	0,42

Live mass determination

Live mass was determined once a week at 08h00 without prior fasting. Although this procedure is recognized as being less reliable due to differential gut full, a period of fasting could interfere with the measurement of "true" *ad lib.* intake. Also, by fitting a mathematical function to the live mass data of several weeks (see Results), the effect of measurement error is reduced, which would render this procedure acceptable.

Digestibility of diets

The object of the digestibility trial was twofold, to determine if apparent digestibility of energy (DE) differs between genotypes at *ad lib.* intake and to determine if DE changes with time. Faeces collections were consequently made every two to three weeks. The calves were distributed at random between weeks of faeces collection with each calf completing at least 4 periods of collection before termination of the growth trial.

Determination of body composition

Body composition was estimated by tritium dilution at 2 to 4 week intervals. In an experiment described by Meissner, van Staden and Pretorius (1980a) tritium (TOH) space was related to water space, lean tissue, protein and fat in the bodies of beef bulls which were kept on the same diets as described here, and which were slaughtered to obtain the amounts of the abovementioned components by chemical analyses. The regression equations obtained are shown in Table 3. The equations presented differ slighly from the published ones. The reason is to ensure complete additivity: As the parameters of regression equations are calculated with error, one often finds that gain in lean tissue (or its components: water, protein and ash) and fat does

Table 3

Prediction equations for components of body composition

Component		Prediction equation	r^2	Mean absolute error (kg)
E.B. Mass_C	=	0,929 L.B. Mass (n = 16)	–	9,84
E.B. Mass_R	=	0,884 L.B. Mass (n = 6)	–	4,47
ln (E.B. Protein)	=	$1{,}209 \ln (\text{TOH})_{5\ \text{min.}} - 2{,}259$	0,988	2,91
E.B. Lean	=	$0{,}703\ \text{TOH}_{5\ \text{min.}} + 0{,}433$ E.B. mass	–	7,21
Calculated equations				
E.B. Fat (kg)	=	E.B. Mass – E.B. Lean		
E.B. Energy (MJ)	=	23,8 E.B. Protein + 39,7 E.B. Fat		

E.B.	Empty body
L.B.	Live body
$\text{TOH}_{5\ \text{min}}$	TOH space as calculated from the 5 minute post-infusion blood sample
C	concentrate diet
R	roughage diet

not add up to gain in empty body mass. Therefore, as shown in Table 3, empty body mass and lean tissue for example, were calculated from regression and fat by subtraction.

It could be argued that both protein and lean tissue should be calculated from an allometric (or log-log) equation instead of the procedure adopted in Table 3. The reasons for the adopted procedure were discussed above and the question is if the estimates of protein were unduely biased within the limits of the experiment. Consequently, protein was calculated by the equation proposed by Robelin & Geay (1978):

$$\text{Protein (kg)} = 0{,}1531 \ \text{Lean tissue}^{1{,}06},$$

and compared to the present estimates. As an example, the values of the Herefords in Appendix 1.1 are compared to the values calculated from the above equation. The results shown in Table 4 are obviously in close agreement.

Procedure of tritium analysis

The methods of Meissner and Bieler (1975) were employed except that the animals were not fasted before administration of the TOH solution. Feed and water were, however, withheld during the period of distribution.

TOH, in a 0,9% NaCℓ carrier solution, was injected intravenously with a sterilized disposable syringe between 08h00 and 09h00. The solution contained about 200 μCi/g TOH of which an accurately determined total amount of 30 - 40 $\mu Ci/W_{kg}^{0,75}$ was injected. Jugular blood samples were taken prior to injection and at 5 min. and 6 h post administration respectively, and stored at 4°C until analysed. From the 5 min. sample apparent empty body water can be calculated (Meissner *et al.* 1980 a) and the 6 h sample enables calculations of the sum of the empty body water and the water in the gut. As gut fill was eliminated by a regression equation between live mass and empty body mass (Table 3), TOH space was calculated only from the 5 min. sample while the 6 h sample was kept as a reserve in case analysis of the 5 min. sample failed.

TOH was quantitatively recovered from the blood samples by vacuum sublimation. The specific activity of the TOH was measured in a Packard Liquid scintillation counter using 1,0 g duplicate aliquots of radio-active water in 10 mℓ scintillation liquid as described by Meissner & Bieler (1975). Apparent TOH space was calculated from the ratio of TOH injected to the concentration at 5 min. or 6 h after correction for pre-injection values. No correction was made for evaporative and urinal losses of TOH which might have occurred during the 6 h following administration.

Table 4

Comparison of the present method of protein calculation with that of Robelin & Geay (1978)

Lean tissue (kg)	Protein (kg) (present)	Protein (kg) (Robelin & Geay)	Difference (kg)
81,6	14,4	16,3	+ 1,9
159	31,4	33,0	+ 1,6
234	49,0	49,7	+ 0,7
308	67,1	66,5	– 0,6
382	86,0	83,6	– 2,4

Animal health

Prolonged feeding with diet C caused digestive upsets and some incidence of bloat in a few animals. This was particularly apparent in the Afrikaners which according to general experience, are known to handle concentrates less well than most genotypes. Only the data of those animals which visually appeared to be in good health were included in the analyses. Their numbers are shown in Table 1.

Statistical analyses

Differences between genotypes and diets were established by means of an analysis of variance procedure.

Results and Discussion

Apparent digestibility of energy (DE)

Time did not significantly affect DE either when tested for on a within animal basis or when tested for on a within genotypic basis. For the analysis of between genotype and dietary differences the results of individuals (i.e. about 4 DE figures) were pooled. It was evident that within animal variation was of the same order and sometimes even larger than variation between genotypes. As a consequence differences between genotypes within a diet were not significant as indicated in Table 5. This is in accordance to most reports (Church, 1975; Schneider & Flatt, 1975) and confirms that differences in digestibility do not contribute appreciably to genotypic variation in growth and efficiency. On the other hand, differenced in DE between diets C and R were highly significant, the actual means corresponding very closely to the estimated figures reported in Table 2. There was also no evidence of significant genotype-dietary interactions in DE.

Cumulative DE intake with time

A suitable function to describe cumulative intake, live mass or body composition with time is the log autoregressive function (Roux, 1976; Meissner, 1977).

Table 5

The apparent DE percentage with genotypes and diets as variables

Genotype	Diet C		Diet R		F-values for differences between		
					Diets	Genotypes	Interaction
Afrikaner	67,7	2,9	59,6	3,2	133***	0,74	0,06
Hereford	68,9	2,5	60,6	1,1			
Simmentaler	68,6	1,0	59,9	0,9			

*** $p < 0{,}001$

Cumulative feed intake (v (t)) etc. is observed in temporal sequence on the same animal. If $\ln(v(t)) = x(t)$, the growth of x at times t and t - 1 is described by:

$$x(t) = \alpha(1-\rho) + \rho x(t-1) + \varepsilon(t), \qquad 2.1$$

where

α = x at t_∞

$\ln\rho$ = relative growth rate of x

$\varepsilon(t)$ = error term

The parameters of Equation 2.1 can be estimated by ordinary least squares procedures.

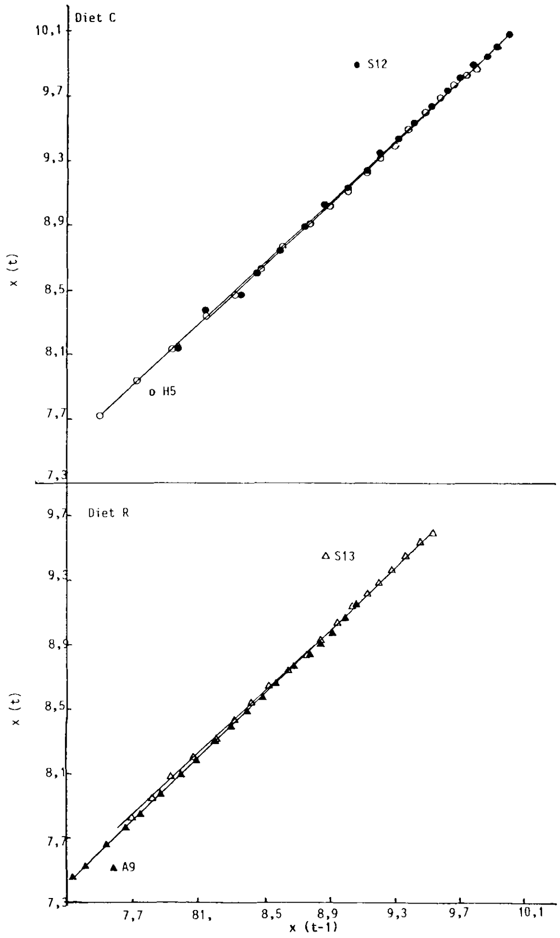

Fig. 1 *Autoregression of ln (cumulative DE intake) for 4 individuals selected at random*

Since cumulative DE intake is measured with less error than live mass or the components of body composition and also has the largest span on the log scale, it is a better procedure to calculate the parameters of ln (cumulative DE intake) by autoregression and to derive the ones of live mass or the components of body composition from these (Roux, pers. comm.).

Such a procedure was followed on the data of every individual. Examples of the accuracy of fit of cumulative DE intake at times t vs t - 1 for a few randomly selected individuals are shown in Fig. 1. The accuracy is clearly exceptional.

The "breaks" in the lines apparently reflect changes in the metabolism of all mammals (von Bertalanffy, 1960; Meissner, 1977; Scholtz & Roux, 1981). These are more clearly illustrated in Fig. 2.

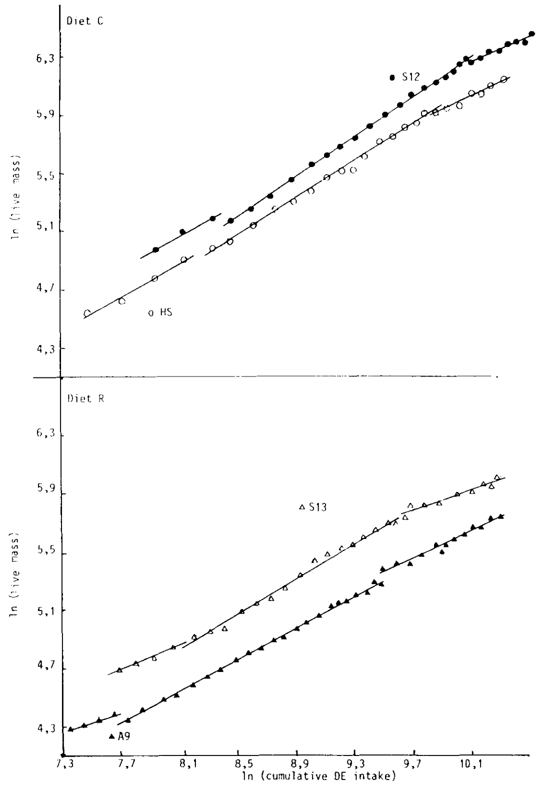

Fig. 2 *Plots of ln (cumulative DE intake) vs ln (live mass) for 4 individuals selected at random*

The solution to equation 2.1 can be written as:

$$x(t) = \alpha - (x(o) - \alpha)\ \rho t, \qquad 2.2$$

where

$$x(o) = x(t) \text{ at } t_o.$$

The procedure to calculate intake, gain, protein and fat deposition, energy retention etc. per day was through differential calculus.

Cumulative DE intake vs live mass or body composition

An allometric equation holds between cumulative DE intake and live mass or the components of body composition (Roux, 1976; Meissner, 1977). If $x_1(t) = \ln v(t)$ and $x_2(t) = \ln w(t)$, where v and w respectively represents cumulative DE intake and body mass, then we have:

$$x_2 = a + bx_1, \qquad 3.1$$

where

$$b = \frac{\beta_2}{\beta_1} \text{ and } a = (\alpha_2 - \frac{\beta_2}{\beta_1} \alpha_1)$$

Equation 3.1 is of course the allometric equation in linearised form.

Plots of the data of the same individuals used in Fig. 1 for ln (cumulative DE intake) vs ln (live mass) and ln (cumulative DE intake) vs ln (TOH space) are depicted in Figs. 2 & 3 respectively. TOH space was used in the regression analyses instead of the components of body composition such as protein or fat, because it was the variable actually measured, while protein and fat were derived from the relationships in Table 3.

Although less accurate than the fit in Fig. 1, a linear equation gives an excellent description of the log transformed data.

Because of larger measurement error in the case of TOH space, the breaks in the lines, as depicted in Fig. 2, were not distinguishable in Fig. 3 and consequently ignored in the plots.

Concept of parameter analysis

The principals are described by Meissner (1977) and Meissner & Roux (this edition). The parameters, ρ, α and x (o) in Equation 2.2 and a and b in Equation 3.1 were substituted for the growth data and the analysis of variance procedures done on them. See Tables 1, 2 & 3 in the paper by Meissner & Roux this edition.

Briefly the parameter ρ * differed highly significantly between genotypes and diets. The parameter α differed highly significantly between genotypes, while the parameter x (o) differed the other way round. If the consequences of these differences are considered in the context of Equation 2.3, it means that voluntary DE intake, gain in body mass, protein and fat deposition and energy retention differed between genotypes and diets. These figures are in Appendices 1.1 and 1.2.

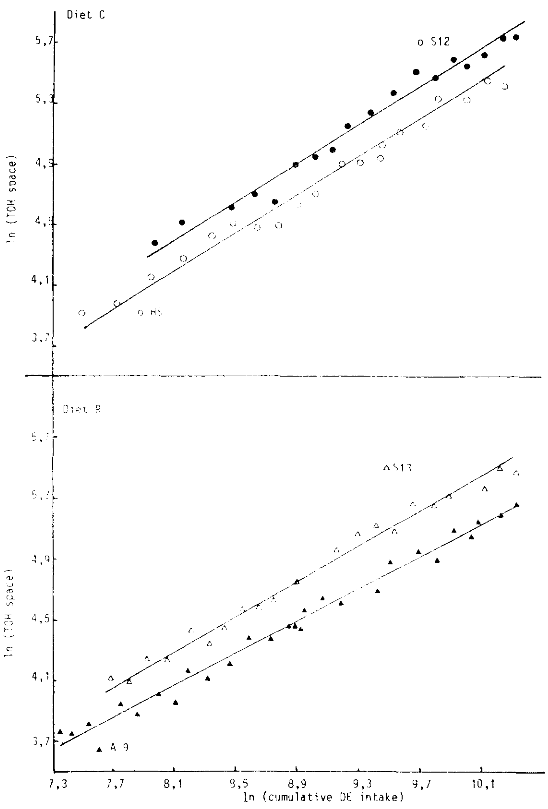

Fig. 3 *Plots of ln (cumulative DE intake) vs ln (TOH space) for individuals selected at random*

In Equation 3.1 the parameter b differed highly significantly between diets but not significantly between genotypes. Following an estimate of a common b within diet an analysis of variance procedure on the adjusted parameter's a revealed highly significant differences between diets and genotypes (see Meissner & Roux, this edition). Due to the fact that the parameters b did not differ between genotypes within diet, it follows that the differences between genotypes on the log scale stayed the same or, on the arithmetic scale, remained the same proportion throughout the growth phase studied. This also applies to the measure of efficiency developed below in (4.1) and (4.2).

If

$$w = cv^b, \qquad 4.1$$

where

w = body mass

v = cumulative feed intake.

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* γ is used in the paper by Meissner & Roux (this edition) instead of ρ. The relationship between γ and ρ is: $\gamma = -\ln\rho$

Then

$$\frac{dw}{dv} = cbv^{b-1},$$

or

$$\frac{dw}{dv} = b\frac{w}{v}. \qquad 4.2$$

Equation 4.2 describes a measure of efficiency in terms of mass produced per unit of feed intake.

Comparison of growth and efficiency in genotypes

The means of a number of relevant observations as calculated by Equations 2.1 to 4.2 are shown in Table 6. A percentage of the exponent α_{mass}, for convenience called "mature mass", was used as basis of comparison in order to approximate "physiological age". The growth interval considered was that between 20 and 60% of mature mass.

The estimated mature mass of 540 kg for the Afrikaner on Diet C appears surprisingly low (Table 6). As discussed under the heading "Animal Health" in "Materials & Methods", the Afrikaners were more prone to digestive upsets on Diet C than the Herefords and Simmentalers which ties in with the general experience that this genotype is more sensitive to the deleterious effects of high concentrates than most exotic breeds. In severe cases this even finds expression in a high incidence of laminitis. Lack of appetite is a usual consequence and this was also evident here as can be seen from Table 6 (see also Appendix 1.1). On the other hand intake on Diet R was quite normal and even appeared slightly higher in the particular interval studied, giving some substance to the claim of many farmers that the Afrikaner is a "roughage feeder".

The Herefords were the fattest on both Diet C and Diet R with the Afrikaners in between and the Simmentalers having the least fat. All genotypes were fatter on Diet C than on Diet R in accordance to many reports (Moulton, *et al.,* 1922; Andersen, 1975; Langholz, 1976; Ferrell, Kohlmeier, Crouse & Hudson Glimp, 1978; Byers & Parker, 1979; Byers & Rompala, 1980). The highest percentage lean and, consequently, protein

Table 6

Mean growth variables calculated for the growth interval 20 to 60% of mature mass

Variable and unit of measurement	Diet C			Diet R		
	Afrikaner	Hereford	Simmentaler	Afrikaner	Hereford	Simmentaler
Mature mass (exp§ α) (kg)	540	704	844	742	708	895
E.B.$^{\Delta}$ mass at 0,4 mature mass (kg)	200	262	314	262	250	316
Cumulative DE intake (MJ)	12353	13925	15021	27531	20208	24066
% protein at 0,4 mature mass	17,5	17,6	19,1	19,1	18,8	20,5
% fat at 0,4 mature mass	14,3	15,7	13,7	13,0	13,6	11,9
% lean at 0,4 mature mass	85,7	84,3	86,3	87,0	86,4	88,1
* DM intake (g/d)	198	222,0	225	101	98,9	93,0
DE intake (KJ/d)	2495	2799,0	2833	1116	1088	1024
ME intake (0,82 DE) (KJ/d)	2048	2294,0	2323	915	892	839
Gain in E.B. mass (g/d)	31,6	39,3	40,7	8,22	10,3	10,0
Gain in E.B. protein (g/d)	5,39	7,11	8,26	1,69	2,14	2,32
Gain in E.B. fat (g/d)	6,94	8,32	7,62	1,44	1,73	1,42
Gain in E.B. lean (g/d)	24,6	31,0	33,0	6,77	8,57	8,60
* Gain in E.B. energy (KJ/d)	404	500	499	97,4	120	112
% of ME retained	19,7	21,8	21,5	10,6	13,5	13,3
% of ME lost	80,3	78,2	78,5	89,4	86,5	86,7
g DM/g E.B. mass gain	6,27	5,65	5,53	12,3	9,60	9,30
KJ ME/KJ gain in E.B. energy	5,07	4,59	4,65	9,39	7,43	7,49

§ Exp. α: Mature mass was assumed to be the exponent of α_{mass} in the description of ln (live mass) with time (corresponding to Equation 2.2).

Δ E.B. mass: Empty body mass.

* All figures expressed in 'per day' were corrected for size using 0,4 $(\exp \alpha_{mass})^{0,58}$ for Diet C and 0,4 $(\exp \alpha_{mass})^{0,72}$ for Diet R (see Appendix 2 for explanation).

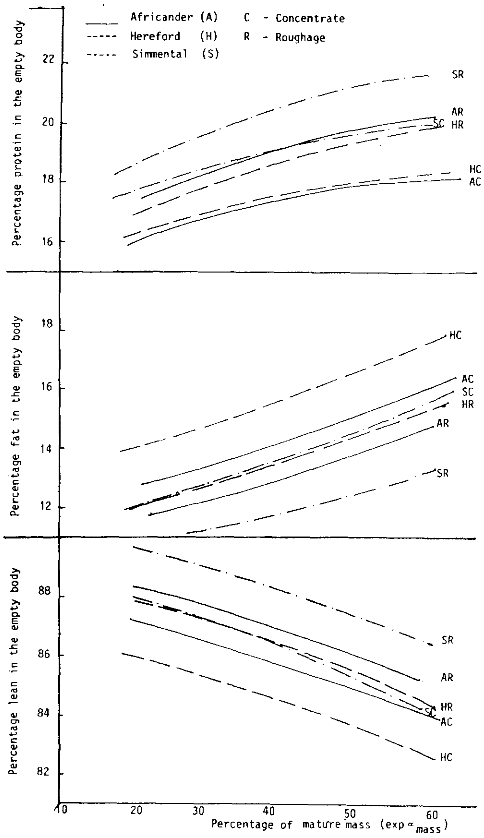

Fig. 4 *Changes in body composition with increasing percentage of mature mass*

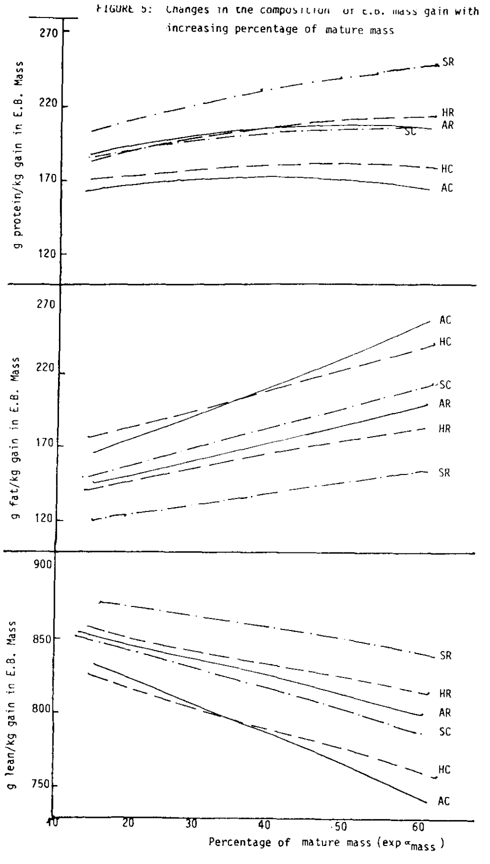

Fig. 5 *Changes in the composition of E.B. mass gain with increasing percentage of mature mass*

was recorded for the Simmentalers (large frame), the Afrikaners (usually medium frame) were intermediary, while the Herefords (small frame) had the lowest lean and protein percentages. Percentage lean was higher on Diet R than on Diet C and in contrast to a number of reports (Béranger, 1976; Byers & Parker, 1979; Byers, 1980) there was no indication of genotype-dietary interaction between the large and small frame types with regard to body composition. Meissner & Roux (this edition) discuss the intricate issue of interaction.

For clearer evaluation, the development of percentage lean, protein and fat with percentage mature mass is illustrated in Fig. 4.

DE and DM intakes of the Herefords and Simmentalers were quite similar on Diet C, with the intakes of the Afrikaner about 12% lower (Table 6). In contrast, the Afrikaner on Diet R showed the highest intake of the 3 genotypes.

Low voluntary intake by indigenous African cattle compared to exotic breeds has been proposed as a possible reason to explain their lower gain and efficiency (Rogerson, Ledger & Freeman, 1968; Ledger, Rogerson & Freeman, 1970), but clearly it does not explain all variation, because despite a higher intake on Diet R, the Afrikaners still realized only about 82% of the gain in E.B. mass achieved by the other 2 genotypes. Another possible explanation appears to be found in the composition of E.B. mass gain as depicted in Fig. 5.

Although the Herefords had the highest percentage fat in their bodies on both diets, the development of fat in E.B. mass gain was slower than that of the Afrikaners, while the percentage gain in fat was substantially lower for the Simmentalers. A fast development of fat in gain is known to eventually affect E.B. mass gain detrimentally (Rogerson *et al.*, 1968; Béranger, 1976; Meissner, 1977; Meissner & Pretorius, 1980), possibly further explaining the slower gains of the Afrikaners.

The most profound effect on gain in E.B. mass could however, probably be explained by the differences in the amount of energy (ME) lost between the Afrikaners and the other 2 genotypes. The Afrikaners lost more on both diets. This is clearly illustrated in Fig. 6.

Part of the energy lost is what is conventianally known as maintenance expenditure. It has been calculated by Van der Merwe & Van Rooyen (1979) that the maintenance needs of the Afrikaner are lower than that of the Simmentaler and this has also been suggested through fasting metabolism studies by Frisch & Vercoe (1977) on Afrikaner crosses and some other breeds. Rogerson in Kenya (Rogerson *et al.*, 1968) also reported a lower fasting metabolism for a number of other indigenous African breeds, but when Ledger (1977) compared the maintenance energy requirements of exercised steers of these very same breeds with that of exotic crossbreds, the latter consistently showed lower requirements. The reports are therefore, conflicting. The reasons are unknown, although the method of comparison could play a role. Some authors did not compare at the same physiological (metabolic) age (say at the same percentage of mature mass as proposed by Taylor, 1965). The acceptance of a constant fasting heat production or maintenance energy expenditure in a growing animal is also conceptionally very difficult to justify. The value of these concepts in the interpretation of genotypic differences must therefore be seriously questioned.

The reasons offered above to explain the slower gain of the Afrikaners on both diets also apply to their poorer feed conversion ratios (Table 6).

It would appear that most differences between the Hereford and the Simmentaler disappear if corrections are made for size according to the suggested procedures (Table 6). Intake and E.B. mass gain were very similar as was the case with percentage energy retained and lost, and efficiency in terms of both g DM/g gain in E.B. mass and KJ ME/KJ gain in E.B. energy. Yet, body composition differed markedly (Figs. 4 & 5). The Herefords contained more fat in their bodies on both diets and also accumulated fat at a faster rate while the Simmentalers contained more protein and lean and also accumulated more protein and lean.

Bèranger (1976) postulated that comparisons between genotypes at the same percentage of mature mass or metabolic age reduce the variation in growth and efficiency but do not account for all the variation. He further stated that the main remaining differences are in the composition of gain. The above results for the Herefords and Simmentalers appear to be in accordance with this postulate. The energetic efficiency of protein deposition is lower than that of fat (Bèranger, 1976). Therefore, in terms of energy, animals with a high growth potential such as the large frame types (Simmentaler) would tend to be less efficient than early maturing animals (Hereford) that fatten quickly (Table 6; Fig. 6). However, the energy cost per gram of organic matter is about the same for protein and fat because of the lower energy content of protein (Bèranger, 1976). Moreover, as protein in lean is associated with three times its weight of water, in terms of gain in E.B. mass, efficiency should theoretically increase as protein content of gain increases. Therefore, animals with a high growth potential in lean, such as the Simmentaler (Table 6), would be more efficient than animals with high fattening capacity (small frame Hereford) in terms of E.B. mass gain and gain in lean.

Although the results on growth and efficiency in the Hereford and Simmentaler are not in conflict to the contention of Bèranger (1976), Langholz (1976) and Andersen (1978) with regard to large and small frame types, the differences here appear to be smaller than that eminating from their work. It would appear that comparison if made at the same percentage of mature mass (Taylor, 1965) instead of using any other measure might offer an explanation. For example, it is generally accepted that large frame types have higher basal energy expenditures and therefore possibly also higher maintenance expenditures*, than small frame types if corrections for size are made through metabolic mass ($W_{kg}^{0,75}$) (Andersen, 1978). As pointed out earlier corrections through metabolic mass do not correct to the same physiological age as does a particular percentage of mature mass or the same growth interval as defined by the Roux model. The results here indicate very little differences in energy loss, and presumably maintenance energy expenditure, if corrections were done through percentage of mature mass (Fig. 6). The same applies to voluntary intake (Table 6). Therefore, if energy intake is similar and energy expenditure is similar as in the case of the Simmentalers and Herefords, efficiency would be the same irrespective of body composition differences. This would suggest body composition differences to be a minor source of variation in determining efficiency. A major one would be energy loss as suggested by the results of the Afrikaners (Table 6; Fig. 6) confirming the contention held by Meissner & Pretorius (1980).

Conclusions

On account of the results and deliberations put forward, it could be argued that productivity in terms of mass or carcass gain and especially lean meat production, can be increased through breeding ingenuity without necessarily affecting efficiency detrimentally. Efficiency would surely be affected detrimentally if energy loss is disproportionately high. The higher energy loss of the Afrikaners on both diets show this source of variation in determining efficiency to be an important one to be considered in breeding programs to improve both productivity and efficiency.

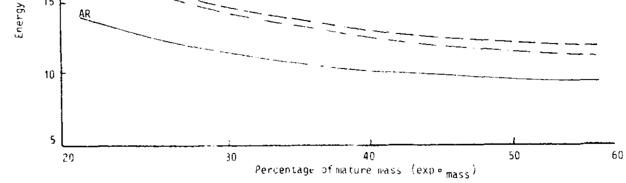

Fig. 6 *Changes in the efficiency of utilization of ME for energy retention with increasing percentage of mature mass*

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* Accepting the way of measurement of these concepts for the moment as valid, see above.

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Appendix 1.1

Data on Diet C

Variable and unit of measurement	Genotype	Live Body Mass (kg)					
		100	200	300	400	500	600
Age (weeks)	Afrikaner	17,3	36,1	53,0	72,8	–	–
	Hereford	13,2	26,7	38,3	50,3	64,3	–
	Simmentaler	–	23,0	33,7	44,2	55,5	68,8
Cumulative DE intake (MJ x 10^3)	A	3,13	9,33	17,7	27,8	–	–
	H	2,47	7,38	14,0	22,0	31,3	–
	S	–	6,28	11,9	18,7	26,6	35,5
Lean in empty body (kg)	A	82,2	160	236	311	–	–
	H	81,6	159	234	308	382	–
	S	–	163	241	318	394	469
Protein in empty body (kg)	A	14,7	31,7	49,7	68,2	–	–
	H	14,4	31,4	49,0	67,1	86,0	–
	S	–	33,4	52,3	72,1	92,5	113,
Fat in empty body (kg)	A	10,7	25,6	42,4	60,7	–	–
	H	11,3	26,6	44,4	63,7	82,5	–
	S	–	22,6	37,4	53,7	70,5	88,4
Energy in empty body (MJ)	A	775	1771	2866	4033	–	–
	H	791	1803	2929	4126	5322	–
	S	–	1692	2730	3848	5000	6199
DE intake (MJ/d)	A	32,9	58,2	65,9	54,2	–	–
	H	34,1	65,5	83,9	87,2	74,5	–
	S	–	61,0	83,0	94,2	93,7	81,1
DM intake (kg/d)	A	2,61	4,62	5,23	4,30	–	–
	H	2,71	5,20	6,66	6,92	5,91	–
	S	–	4,84	6,59	7,48	7,44	6,44

Appendix 1.1 (Continued)

Variable and unit of measurement	Genotype	Live Body Mass (kg)					
		100	200	300	400	500	600
Gain in live body mass (kg/d)	Afrikaner	0,70	0,86	0,81	0,63	–	–
	Hereford	0,91	1,19	1,23	1,13	0,91	–
	Simmentaler	–	1,26	1,37	1,33	1,18	0,86
kg DM/kg gain in live body mass	A	3,73	5,37	6,46	6,83	–	–
	H	2,98	4,37	5,41	6,12	6,49	–
	S	–	3,84	4,81	5,62	6,25	–
Gain in empty body lean (kg/d)	A	0,54	0,63	0,57	0,42	–	–
	H	0,70	0,89	0,90	0,81	0,63	–
	S	–	0,98	1,04	1,00	0,87	0,69
Gain in empty body protein (kg/d)	A	0,11	0,14	0,13	0,09	–	–
	H	0,14	0,20	0,21	0,19	0,15	–
	S	–	0,23	0,26	0,26	0,23	0,18
Gain in empty body fat (kg/d)	A	0,11	0,16	0,18	0,16	–	–
	H	0,14	0,21	0,24	0,24	0,21	–
	S	–	0,19	0,23	0,24	0,23	0,20
Gain in empty body energy (MJ/d)	A	6,98	9,72	10,1	8,62	–	–
	H	8,91	13,2	14,7	14,1	12,0	–
	S	–	13,1	15,3	15,7	14,6	12,3
% ME retained (ME = 0,82 DE)	A	25,9	20,4	18,7	19,4	–	–
	H	31,9	24,6	21,4	19,7	19,6	–
	S	–	26,2	22,5	20,3	19,0	18,5
% ME lost	A	74,1	79,6	81,3	80,6	–	–
	H	68,1	75,4	78,6	80,3	80,4	–
	S	–	73,8	77,5	79,7	81,0	81,5
MJ ME/MJ gain in empty body energy	A	3,87	4,91	5,35	5,16	–	–
	H	3,14	4,07	4,68	5,07	5,09	–
	S	–	3,82	4,45	4,92	5,26	5,41

Appendix 1.2

Data on Diet R

Variable and unit of measurement	Genotype	Live Body Mass (kg)					
		100	200	300	400	500	600
Age (weeks)	Afrikaner	22,8	50,2	73,4	96,5*	–	–
	Hereford	14,7	36,7	55,4	74,3	95,4	–
	Simmentaler	–	30,7	48,0	64,3	81,0	88,5
Cumulative DE intake (MJ x 10^3)	A	3,55	11,6	23,3	38,2	–	–
	H	2,75	9,02	18,1	29,6	43,4	–
	S	–	7,57	15,2	24,9	36,4	49,8
Lean in empty body (kg)	A	79,3	156	231	306	–	–
	H	78,6	155	229	303	377	–
	S	–	159	235	311	387	462
Protein in empty body (kg)	A	14,2	31,7	50,1	69,8	–	–
	H	13,9	31,0	49,4	68,2	88,4	–
	S	–	33,1	52,3	72,9	94,1	116,0
Fat in empty body (kg)	A	9,1	20,8	34,2	47,6	–	–
	H	9,8	21,8	36,2	50,6	65,0	–
	S	–	17,8	30,2	42,6	55,0	68,4
Energy in empty body (MJ)	A	699	1580	2550	3550	–	–
	H	720	1603	2613	3632	4684	–
	S	–	1494	2444	3426	4423	5476
DE intake (MJ/d)	A	25,1	53,7	74,1	82,3	–	–
	H	24,4	51,9	71,0	77,7	70,0	–
	S	–	47,5	69,6	84,1	89,3	84,2
DM intake (kg/d)	A	2,28	4,88	6,74	7,48	–	–
	H	2,22	4,72	6,46	7,06	6,36	–
	S	–	4,32	6,33	7,65	8,12	7,66

* Figures beyond 80 weeks of age are extrapolations.

Appendix 1.2 (Continued)

Variable and unit of measurement	Genotype	Live Body Mass (kg)					
		100	200	300	400	500	600
Gain in live body mass (kg/d)	Afrikaner	0,44	0,59	0,63	0,60	–	–
	Hereford	0,55	0,73	0,78	0,73	0,62	–
	Simmentaler	–	0,78	0,87	0,88	0,82	0,72
kg DM/kg gain in live body mass	A	5,18	8,27	10,7	12,5	–	–
	H	4,04	6,47	8,28	9,67	10,3	–
	S	–	5,54	7,28	8,69	9,90	10,6
Gain in empty body lean (kg/d)	A	0,33	0,44	0,46	0,43	–	–
	H	0,42	0,55	0,57	0,53	0,44	–
	S	–	0,60	0,66	0,66	0,62	0,54
Gain in empty body protein (kg/d)	A	0,07	0,10	0,12	0,11	–	–
	H	0,09	0,13	0,14	0,14	0,12	–
	S	–	0,15	0,17	0,18	0,18	0,16
Gain in empty body fat (kg/d)	A	0,05	0,08	0,10	0,10	–	–
	H	0,07	0,10	0,11	0,11	0,10	–
	S	–	0,09	0,11	0,11	0,11	0,10
Gain in empty body energy (MJ/d)	A	3,77	5,71	6,55	6,60	–	–
	H	4,73	6,99	7,91	7,81	6,96	–
	S	–	6,89	8,29	8,74	8,66	7,67
% ME retained (ME = 0,82 DE)	A	18,3	11,0	10,8	9,78	–	–
	H	23,6	16,4	13,6	12,3	12,1	–
	S	–	15,0	14,5	12,7	11,8	11,1
% ME lost	A	81,7	89,0	89,2	90,2	–	–
	H	76,4	83,6	86,4	87,7	87,9	–
	S	–	85,0	85,5	87,3	88,2	88,9
MJ ME/MJ gain in empty body energy	A	5,46	7,71	9,28	10,2	–	–
	H	4,23	6,09	7,36	8,16	8,25	–
	S	–	5,65	6,88	7,89	8,46	9,00

Appendix 2

Correction for size was done by dividing by the mean body mass figure within this interval, i.e. 40% of mature mass, but employing the power of 0,58 in the case of Diet C and 0,72 in the case of Diet R. This procedure renders direct comparison between the diets invalid.

The procedure of dividing by $W^{0,58}$ and $W^{0,72}$ instead of the more conventional $W^{1,0}$ or $W^{0,75}$ seems odd. However, since a number of factors may influence the relevant power, the best procedure is to calculate the one directly applicable in the particular experiment. The relevant power can be obtained from the allometric equation between cumulative feed intake and body mass:

If

$$w = cv^b$$

as in Equation 4.1, then

$$v = c^{-1} w^{\frac{1}{b}}$$

and

$$\Delta v = (c^{-1}) (\frac{1}{b}) w^{\frac{1}{b} - 1} \ . \ \Delta W$$

where

Δv = rate of intake, e.g. intake per day

Δw = rate of body mass gain, e.g. gain per day

The power $\frac{1}{b} - 1$ depicts the directly applicable one. In one of the growth phases under consideration b for example was equal to 0,634 on Diet C and 0,583 on Diet R (see Meissner & Roux, this edition). On Diet C, therefore,

$$\frac{1}{b} - 1 = \frac{1}{0,634} - 1 = 0,58$$ and on Diet R,

$$\frac{1}{b} - 1 = \frac{1}{0,583} - 1 = 0,72$$